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Taxonomic and functional diversity patterns of multi-taxa in Mediterranean wood-pastures

"Documento Definitivo"

Doutoramento em Biodiversidade, Genética e Evolução

Duygu Pembe Oksuz

Tese orientada por:
Professor Doutor Jorge Manuel Mestre Marques Palmeirim
Doutor Ricardo Aleixo Henriques Correia

Documento especialmente elaborado para a obtenção do grau de doutor

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Notas prévia

A presente tese apresenta artigos científicos prontos para serem submetidos (capítulos 2 a 5), de acordo com o previsto no nº 2 do artigo 25º do Regulamento de Estudos de Pós-Graduação da Universidade de Lisboa, publicado no Diário da República, 2.ª série — N.º 57 — 23 de Março de 2015. Uma vez que estes trabalhos foram realizados em colaboração o candidato esclarece que participou integralmente na conceção dos trabalhos, preparação de dados, análise e discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, Julho de 2019

Duygu Pembe Oksuz

To Sibel Arslan

"What is the Mediterranean? One thousand things at a time. Not just one landscape, but innumerable landscapes. Not just one sea, but a succession of seas. Not just one civilization, but many civilisations packed on top of one another. The Mediterranean is a very old crossroads. Since millennia, everything converged on it."
Fernand Braudel , 1985

" ...Perhaps niche will turn out to be a concept that requires some subdivision into several precise definitions."
Robert MacArthur , 1972

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Abstract

A long-term history of multi-functional management and natural disturbances have transformed many woodlands of Europe into unique landscapes that integrate forests, open grazed pastures with scattered shrubs and trees, in addition to various semi-natural vegetation elements. These landscapes, named wood-pastures, often represent economically valuable and biodiversity-rich habitats with a characteristic semi-open and heterogeneous vegetation structure and can be found throughout different European bioregions. In the Western Mediterranean the most important types of wood-pastures have a tree cover dominated by oaks and are known as “montados” (in Portugal) and dehesas (in Spain). Wood-pastures are increasingly fragile due to conflicting land-use regimes associated with intensification and abandonment, which influence vegetation structure and overall habitat heterogeneity leading to impacts on biodiversity and ecosystem processes. This situation highlights the urgent need to improve low-cost and biodiversity-friendly management strategies that have minimal negative effects on production to preserve the balance between natural and economic values of wood-pastures. The main objective of this thesis, which focuses on Mediterranean wood-pastures, is to explore the biodiversity patterns of multiple taxa using the advantages of functional diversity approaches to reveal how land-use driven changes influence biodiversity, ecosystem functioning and ecosystem services in wood-pastures, and use these insights to improve science-based, sustainable management plans. For these aims, this thesis evaluated the role of small ungrazed patches within the wood-pasture matrix in enhancing (1) taxonomic and (2) functional diversity of multi-taxa (plants, beetles, lichens). The results revealed the contribution of allowing shrub growth within ungrazed patches to species richness and functional diversity of plants, beetles and lichens by facilitating the presence of distinct species and trait assemblages compared to wood-pasture matrix. This work also assessed how changes in habitat structure associated with a management intensity gradient ranging from active management towards land abandonment

affected (3) species and trait assemblages of breeding birds in wood-pastures and (4) of insectivore birds in particular to evaluate the potential consequences for natural pest regulation in wood-pastures. The findings showed the role of sustaining non-intensive and active management, which prevented excessive shrub growth and loss of habitat heterogeneity, in facilitating the distribution of more diverse bird guilds and in potential contributions to the natural pest control provision in wood-pastures. Overall, the key findings of this thesis highlight the importance of maintaining small ungrazed patches and non-intensive, active management strategy to preserve the semi-open and heterogeneous habitat structure that increase biodiversity of plants, beetles, lichens and birds, leading to positive influences on ecosystem functioning and service provision in wood-pastures. Finally, this work contributes to ongoing efforts to improve low-cost and sustainable management actions conciliating the natural and economic values of wood-pastures.

Keywords: wood-pasture; montados/dehesas; taxonomic and functional diversity; habitat management; social-ecological systems

Resumo

Uma longa história de distúrbios naturais e gestão multifuncional transformaram muitas das florestas originais da Europa em paisagens únicas que integram múltiplos elementos, incluindo áreas de floresta, zonas abertas de pastagem com pequenas manchas arbustivas e zonas de vegetação seminatural. Estas paisagens, comumente apelidadas de pastagens arborizadas, podem ser encontradas em várias regiões Europeias e representam com frequência habitats ricos em biodiversidade e de elevado valor económico, apresentando uma estrutura de vegetação semiaberta e heterogénea que lhes é característica. Estas paisagens encontram-se, contudo, numa situação cada vez mais fragilizada devido a mudanças no regime tradicional de uso da terra, tanto por intensificação como por abandono, que influenciam a estrutura da vegetação e a heterogeneidade destes habitats e originam impactos na sua biodiversidade e processos ecológicos. Esta situação gera a necessidade de desenvolver estratégias de gestão da paisagem com baixo custo e impactos mínimos na produtividade económica destes habitats, mas que simultaneamente permitam a manutenção da sua biodiversidade e valores naturais. O principal objetivo deste trabalho, que se foca nas pastagens arborizadas da região Mediterrânica, na sua maior parte montados, é explorar os padrões de diversidade taxonómica e funcional associados a múltiplos grupos biológicos de forma a entender como mudanças na gestão poderão influenciar a biodiversidade, funcionamento do ecossistema e a provisão de serviços ecossistémicos em pastagens arborizadas, e usar esse conhecimento para propor ações de gestão sustentável para estes ecossistemas. Para cumprir este objetivo, foram realizados quatro trabalhos individuais que que são resumidos de seguida.

Capítulo 2. Aumentar a biodiversidade em pastagens arborizadas através da proteção de pequenas manchas de habitat não pastoreado

O trabalho apresentado neste capítulo procurou explorar a contribuição de pequenas manchas de habitat não pastoreado para a composição e riqueza de espécies de múltiplos grupos taxonómicos em áreas de pastagem arborizada (montado). Especificamente, foram amostradas as comunidades

de plantas, besouros e líquenes em 13 pequenas manchas de habitat não pastoreado (252 a 2000m^2) e em 11 locais próximos na matriz de pastagem arborizada. A composição de espécies nos dois tipos de habitat foi comparada com recurso a análises de semelhança (ANOSIM) e de correspondência (CA). Foram também calculadas curvas de rarefação para avaliar a contribuição de áreas não pastoreadas para a riqueza de espécies. Os resultados sugerem que a vegetação arbustiva que se desenvolve nas pequenas manchas de habitat não pastoreado suporta uma assembleia de espécies distinta daquela que é encontrada em zonas pastoreadas, contribuindo para aumentar significativamente a diversidade de espécies. Este trabalho sugere que a preservação, ou mesmo o aumento, da disponibilidade de pequenas manchas de habitat não pastoreado é uma estratégia promissora e de baixo custo para aumentar a diversidade de espécies em pastagens arborizadas, sem comprometer a viabilidade económica deste sistema agro-silvo-pastoril.

Capítulo 3. A contribuição de pequenas manchas de habitat não pastoreado para a diversidade funcional de pastagens arborizadas

Este trabalho comparou a diversidade de traços funcionais de múltiplos grupos taxonómicos observada em pequenas manchas de habitat não pastoreado e na matriz de habitat de pastagens arborizadas (montado) em Portugal. Para isso, foram avaliadas a composição funcional (médias ponderadas para a comunidade) e diversidade funcional (índices de uniformidade e dispersão funcional) de plantas, besouros e líquenes em 13 manchas de habitat não pastoreado (252 a 3000m^2) e em 11 locais de matriz de habitat. Os resultados demonstram que a presença de traços funcionais distintos nas manchas de habitat não pastoreado contribui significativamente para a diversidade funcional de pastagens arborizadas. Especificamente, pequenas manchas não pastoreadas apresentam uma maior proporção de plantas lenhosas, de folha permanente e larga, e com frutos carnudos de dispersão zoocoria, de besouros pequenos e fungívoros e de líquenes fruticosos, folhosos, higrofíticos e oligotróficos. Os resultados indicam também que a dispersão funcional de

plantas e a uniformidade funcional de besouros e líquenes são maiores em manchas de habitat não pastoreado. Estes resultados sugerem que a preservação, ou mesmo o aumento, da disponibilidade de pequenas manchas de habitat não pastoreado podem ser consideradas medidas de baixo custo que contribuem para a diversidade funcional e funcionamento do ecossistema em pastagens arbóreas sem afetar o valor económico destes sistemas.

Capítulo 4. Respostas taxonómicas e funcionais de aves à diminuição da intensidade de gestão em pastagens arborizadas

O objetivo deste trabalho foi explorar de que forma mudanças na estrutura do habitat associadas a um gradiente de gestão representativo de um abandono gradual do uso da terra influenciam a diversidade taxonómica e funcional de aves em pastagens arborizadas da região ibérica e Norte de África. Para isso, foi amostrada a comunidade de aves presente em trinta e sete pastagens arborizadas, distribuídas entre Portugal (N = 17), Espanha (N = 13) e Marrocos (N = 7), durante a época reprodutora. Posteriormente, analisou-se a forma como mudanças na estrutura do habitat influenciaram a riqueza específica, diversidade funcional (riqueza, uniformidade e dispersão funcional) e composição funcional (médias ponderadas para a comunidade) de aves com recurso a modelos lineares. Os resultados sugerem a existência de mudanças na estrutura da vegetação e na heterogeneidade do habitat ao longo do gradiente de gestão avaliado, e que essas mudanças influenciaram a diversidade e composição funcional presente na comunidade de aves, mas não a diversidade taxonómica. Mais especificamente, foram detetadas reduções significativas na dispersão e uniformidade funcional em resposta a um aumento da cobertura e desenvolvimento de arbustos e a uma diminuição da heterogeneidade do habitat. Para além disso, observou-se também uma diminuição da abundância relativa de aves de áreas abertas e generalistas, com hábitos granívoros e de alimentação e nidificação no solo em áreas mais homogéneas e com gestão menos intensiva. Por outro lado, registou-se um aumento significativo na abundância relativa de aves que se alimentam em arbustos e que nidificam e se alimentam na copa das árvores em zonas dominadas

por arbustos, ainda que estas aves estejam também presentes em zonas com gestão mais intensiva. Estes resultados sugerem que a tendência para o abandono de pastagens arborizadas provoca alterações na estrutura do habitat que restringem a presença de aves generalistas ou dependentes de áreas abertas, levando a uma consequente perda de diversidade funcional.

Capítulo 5. O abandono de pastagens arbustivas reduz a diversidade funcional de aves insectívoras com potenciais consequências para o controlo de pragas

Este trabalho investigou a influência de mudanças na estrutura do habitat associadas a um gradiente de intensidade de gestão na diversidade taxonómica e funcional de aves insectívoras em pastagens arborizadas da Península Ibérica e Norte de Africa, e potenciais consequências para o controle de pragas realizado por este grupo biológico. O trabalho procurou responde a duas questões específicas: a) A diversidade taxonómica e funcional de aves insectívoras responde a mudanças na estrutura do habitat associadas com o abandono da terra? b) Como é que traços funcionais de aves associados ao serviço de regulação de pragas variam em relação à estrutura do habitat? Para isso, foi avaliada de que forma a abundância de aves insectívoras, vários índices de diversidade taxonómica (riqueza de espécies e Shannon-Wiener) e funcional (riqueza, uniformidade e divergência funcional), e composição funcional de traços associados a predação de insetos (médias ponderadas para a comunidade) responderam alterações na estrutura do habitat. Foram registados declínios na abundância de aves insectívoras, divergência funcional e na abundância relativa de aves maiores e que se alimentam no solo em áreas dominadas por vegetação arbustiva associadas a um abandono gradual do uso da terra. Os resultados sugerem que uma redução significativa da intensidade de gestão e uso da terra devido ao abandono leva a alterações significativas na estrutura do habitat que resultam numa redução da abundância e diversidade de aves insectívoras em pastagens arborizadas com potenciais consequências negativas para o controlo natural de pragas. De forma geral, os resultados deste trabalho demonstram a importância de preservar sistemas de gestão não intensiva em pastagens arborizadas, onde seja permitida a presença de pequenas manchas de

habitat não pastoreado, de forma a preservar uma estrutura de vegetação semi-aberta e heterogénea que permita a manutenção de comunidades diversas de plantas, besouros, líquenes e aves, o que contribuirá positivamente para o funcionamento do ecossistema e provisão de serviços naturais. Finalmente, com base nos resultados globais obtidos, este trabalho propõe um conjunto de medidas de baixo custo para a gestão sustentável do habitat, por forma a melhorar a conciliação dos valores económicos e naturais de pastagens arborizadas.

Palavras-chave: montados/dehesas; diversidade taxonômica e funcional; gestão de habitats; sistemas sócio-ecológicos; heterogeneidade do habitat

CHAPTER 1

General Background

The major drivers of global biodiversity loss are resource overexploitation and land use intensification, followed by habitat degradation, diseases and pollution, which are often interlinked with the effects of climate change (Pereira et al. 2012; Maxwell et al. 2016; Tilman et al. 2017). Human population growth has driven and accelerated these threats increasing the demand for food and other goods, which induced the expansion of production lands with increased use of mono-cultures and pesticides (Stoate et al. 2009). Moreover, a growing body of evidence shows that biodiversity loss may be leading to further reductions in the provision of ecosystem functions and services (Valiente-Banuet et al. 2015; Allan et al. 2015). All these call for an urgent need to develop strategies of sustainable land-use that conciliate economic development and nature conservation (Titeux et al. 2016; Arosa et al. 2017).

Human-modified landscapes presently cover vast areas worldwide. They are simultaneously important for production and as habitats for a wide range of species, making them a challenge for the conservation of biodiversity (Fischer and Lindenmayer 2006). In these landscapes, well-designed biodiversity-friendly management strategies can be a key to mitigate threats to their biodiversity while maintaining the economic value (Mönkkönen et al. 2014; Hartel et al. 2018). The overall aim of this study is to contribute to the knowledge required to develop such sustainable management strategies in wood-pastures, economically important and biodiversity rich human-modified landscapes.

Wood-pastures

The archetypes of European wood-pastures were wooded landscapes grazed by wild herbivores (Behre 1988; Rackham 1998; Green 2013). Human interaction with these landscapes dates back to the

Neolithic era; it started with livestock grazing (Luick 2009) and continued with cropping, pollarding and logging (Jørgensen 2013; Jørgensen and Quelch 2014). Various species of oak (*Quercus* spp.), pear (*Pyrus* sp.), willow (*Salix* spp.), hornbeam (*Carpinus spp.*) and beech (*Fagus spp.*) are known to have been maintained throughout the 18th and 19th centuries for various uses such as fattening pigs, harvesting fruits or making fences and bindings to support hay (Jørgensen and Quelch 2014). Due to demands resulting from increasing population growth, agricultural activities and timber production intensified, transforming the dense wooded landscapes into more open habitats with scattered trees. This accelerated the separation of the landscape into agricultural fields and areas devoted to forestry, although the integrated habitat structure of semi-open woodlands preserving features of the ancient woodlands has been maintained to some extent across Europe (Bergmeier and Roellig 2014; Hartel et al. 2015).

Since the first human intervention, these landscapes have been exposed to fluctuations in human-use, which included intensive and extensive agriculture, changes in the level of grazing determined by the value of competing products, such as timber and olives, and legal restrictions on livestock raising resulting in a highly dynamic and mosaic habitat structure (Clément 2008; Öllerer 2014; Hartel et al. 2015). Disturbances such as fire, either natural or started by humans to expand croplands, is another factor that changed the vegetation structure and the canopy openness of European landscapes substantially (Blondel et al. 2010a). Thereby, the relic woodlands of Europe evolved under the complex interactions of human-use and natural disturbances into the current landscapes representing a unique integration of closed-canopy forests and open pastures with scattered shrubs and trees covering around 203.000 km2 (4.7%) in total (Plieninger et al. 2015).

These landscapes were defined under various names reflecting the ancient term of "*sylva-saltus-ager* (woodland-pasture-field)" such as "silvopastoral system", which integrates livestock grazing with trees, or "agro-sylvo-pastoral systems" defining the areas where the forestry production and regular grazing co-occurs with agriculture (Clément 2008; Blondel et al. 2010b). Bergmeier et al. (2010) reviewed the common local and regional terms defining these landscapes which include, in addition to wood-pastures, "ancient park", 'savannah', 'semi-open pastureland' and 'traditional orchard'. Although the habitat structure and type of land-use vary to some extent within Europe, the unifying designation of "wood-pasture", which attributes an equal importance to the pasture and woody components of these landscapes, is presently widely used (Hartel and Plieninger 2014a). Given that the ecological and socio-economic factors shaping these landscapes are interlinked, it is important to use a common term to provide a comprehensive recognition and protective status for these valuable systems (Bergmeier et al. 2010; Hartel and Plieninger 2014a).

The long-term interaction between humans and wood-pastures also led to strong social connections between people and the habitat, beyond the economic dependence. Wood-pastures are part of the cultural heritage of Europe, retaining traditional knowledge on nature and human-use throughout generations (Szabó and Hédl 2013). Moreover, this traditional knowledge and its associated collective memory play an important role in land-use decision-making, independent of policy-dependent triggers, and is being recognized as vital to improve conservation of wood-pastures (Roellig et al. 2016; Moreno et al. 2018). Furthermore, these landscapes also provide recreation areas for leisure and ecotourism activities and have an aesthetic value that contributes greatly to the delivery of cultural ecosystem services (Varga and Molnár 2014).

Wood-pastures have broadly similar habitat structures across Europe, despite variations in the density, composition and age of trees and in grazing practices, which result from regional differences in biogeographical features, land-use history and ongoing management strategies (Hartel et al. 2013; Chételat et al. 2013; Plieninger et al. 2015). In general, intensely grazed areas usually feature mostly sparsely distributed large old trees due to the lack of regeneration, whereas areas devoted forestry or abandoned, and thus without regular grazing, are comprised by diverse and dense woody vegetation (Roellig et al. 2018). Thus, depending on the grazing regime and on the other forms of exploitation, the tree density of European wood-pastures can vary from just a few trees up to 500 trees per hectare (Castro 2009; Garbarino and Bergmeier 2014). The tree layer often features a mixed composition of oak trees (*Quercus* spp.), willows (*Salix* spp.), beech (*Fagus* spp.), ash (*Fraxinus* spp.), maple (*Acer* spp.), and poplar (*Populus* spp.) in addition to various fruit trees, but this varies regionally. In the Mediterranean region, the tree layer is usually mostly dominated by oak species (Roellig et al. 2018). Old-growth English oaks (*Q. robur*) and sessile oaks (*Q. petraea*) are often found in high densities in Eastern Europe and particularly in Romanian wood-pastures where grazing is also common. However, grazing is generally prohibited in Hungarian pastures (Hartel et al. 2013; Moga et al. 2016). The tree layer is usually composed by high densities of birches (*Betula* spp.) and conifers (*Pinus* spp., Picae spp.) together with English oak (*Q. robur*) and sessile oak (*Q. petraea*) in northern Europe, where wood-pastures are often devoted to reindeer husbandry and timber production in Sweden (Moreno et al. 2018). Wood-pastures are mostly comprised of dense forests and conserved parklands in UK (Rotherham 2007). In central Europe, wood-pastures are mostly represented by hedged meadows in Germany (Luick 2009), although most of them are abandoned and in France, where the main management activities are planting hedges, pruning and pollarding (Moreno et al. 2018). In Greece, wood-pastures are dominated by the deciduous Valonia oak (*Q. ithaburensis subsp. macrolepis*) and downy oak (*Q. pubescens*) and are often sustained by grazing in various degrees of intensity (Kizos et

al. 2013). In Italian wood-pastures, used for grazing by sheep and cattle, the tree layer is dominated by Holm oak (*Q. ilex*), cork oak (*Q. suber*) and downy oak (*Q. pubescens*) (Eichhorn et al. 2006).

Iberian wood-pastures are among the most extensive wood-pastures in Europe, covering vast regions in Portugal, where they are usually called *montados,* and in Spain, where they are referred to as *dehesa*s. In these regions, wood-pastures are usually managed by large private estates (Joffre et al. 1999; Olea and San Miguel-Ayanz 2006; Pinto-Correia et al. 2011). These landscapes are often dominated by cork oak (*Q. suber*) and holm oak (*Q. rotundifolia*), often co-occurring with Algerian oak (*Q. canarensis*), Pyrenean oak (*Q. pyrenaica*), mastic tree (*Pistacia lentiscus*) and wild olive (*Olea europaea* var. *sylvestris*) (Bugalho et al. 2009; Bergmeier et al. 2010). *Montados* and *dehesa*s are usually recognised as economically viable examples of wood-pastures that are well-adapted to multiple types of land-use (Blondel et al. 2010b). Pigs, sheep and increasingly cattle graze these systems (Clément 2008; Castro 2009; Pinto-Correia et al. 2011). Cork extraction is also a major exploitation in cork oak dominated wood-pastures; the Iberian Peninsula generates the highest economic revenue from cork extraction worldwide, especially Portugal, which provides 51% of the global cork production (Costa et al. 2011). Meat, cheese and cereals are also among the most valued production of these systems, while cropping and pruning can also be important providing animal fodder, firewood and, less commonly, charcoal. In addition, collection of pine seeds, mushrooms, resins, wild fruits, aromatic and medical plants, and beekeeping are still practised (Berrahmouni et al. 2007; Moreno and Pulido 2009; Sá-Sousa 2014).

Similar landscapes cover parts of the African side of the Mediterranean basin in Algeria, Morocco and Tunisia, where in some regions they are named *azaghar* (Bugalho et al. 2009). Atlas cedar (*Cedrus atlantica*), Pyrenean oak (*Q. pyrenaica*) and maritime pine (*Pinus pinaster*) are the prevalent tree species in these wood-pastures at higher altitudes, whereas cork oak (*Q. suber*), holly oak (*Q. coccifera*), Algerian oak (*Q. canariensis*) and holm oak (*Q. rotundifolia)* are found in lower elevations,

along with the endemic pear (*Pyrus bourgaeana* subsp. *mamorensis*), argan tree (*Argania spinosa*) and local varieties of olive tree (*Olea europaea* and *O. maroccana*) (Ajbilou et al. 2006; Bugalho et al. 2009). North African wood-pastures are often grazed by sheep, goats and cows, alongside cork extraction. Charcoal production is still widespread in North Africa, although it almost ceased in Iberian wood-pastures (Berrahmouni et al. 2007; Bugalho et al. 2009). Additionally, tree oil extraction such as argan oil can also generate high revenue and is also a common activity in North-Africa. Transhumance, the seasonal movement of livestock by shepherds, can still be found in some areas and helps to maintain grazing in both low- and high-altitude North-African pastures (Berrahmouni et al. 2007; Oteros-Rozas et al. 2014).

The mosaic vegetation structure of wood-pastures, which often includes closed forests, open grasslands, agricultural fields and a variety of semi-natural landscape elements such as riparian galleries, olive orchards, hedgerows and ungrazed areas, fosters spatial heterogeneity at multiple landscape scales (Simonson et al. 2018; Galle et al. 2017). The high vegetation heterogeneity often found in these areas provides distinct micro-habitats conditions in terms of shade, temperature, moisture and soil nutrients (Garbarino and Bergmeier 2014; Schmidt et al. 2017; Erdős et al. 2018b) and results in an enhanced diversity of feeding and nesting resources, shelter availability and habitat connectivity, which contributes to the high biodiversity of these landscapes (Santos-Reis and Correia 1999; Hartel et al. 2014; Simonson et al. 2018). For example, wood-pastures often have a diverse tree layer, both in terms of species composition and ages, in addition to native shrubs and a high diversity of herbaceous plants (Bergmeier et al. 2010; Garbarino and Bergmeier 2014). Moreover, the vegetation of riparian galleries found in these landscapes also contributes to this diversity, usually featuring other tree species, such as narrow-leaved ash (*Fraxinus angustifolia*), alder (*Alnus* spp.), willow (*Salix* spp.), or poplar (*Populus* spp.), and a highly diverse shrub community (Corbacho et al. 2003). Small olive

orchards and riparian galleries enhance species diversity of mammals (Diaz et al. 1997; Rosalino et al. 2009), arthropods (Taboada et al. 2006; Silva et al. 2009) and birds (Godinho et al. 2010; Leal et al. 2011) in wood-pastures. Ancient veteran trees are also crucial habitat for several species of lichens (Johansson et al. 2007), fungi (Blasi et al. 2010) and beetles (Falk 2014; Parmain and Bouget 2018). Hedgerows, usually maintained to protect croplands from livestock, contribute to shrub diversity and increase refuge availability and habitat connectivity, especially for species with limited dispersal capacity (Lecq et al. 2017; Graham et al. 2018). Ungrazed patches of herbaceous vegetation have been shown to enhance invertebrate species diversity (Bugalho et al. 2011b). Another semi-natural element of wood-pastures are shrubby patches, which are usually associated to rocky outcrops or other elements that prevent grazing and mechanical shrub clearing, allowing the regeneration of native shrubs (Smit et al. 2005; Barroso et al. 2012). Moreover, a well-developed native vegetation has been shown to promote beneficial arthropods contributing to pests control (Tscharntke et al. 2002; Isaacs et al. 2009).

Besides their capacity to maintain high-levels of species diversity, wood-pastures are also known to be an umbrella habitat hosting several endangered or rare species and subspecies (Diaz et al. 1997; Bergmeier and Roellig 2014). For instance, Hungarian wood-pastures are priority habitats for local endemic plants such as *Paeonia officinalis* subsp. *banatica* and *Pulsatilla pratensis* subsp. *nigricans*. These species are similar to shade-tolerant species of *Paeonia* spp. and *Helleborus* spp. which are reported to be regionally specific to Greek wood-pastures (Chaideftou et al. 2009; Bergmeier and Roellig 2014). Furthermore, Mediterranean wood-pastures are important habitats for Iberian lynx (*Lynx pardinus*), Iberian imperial eagle (*Aquila adalberti*), black stork (*Ciconia nigra*), Eurasian crane (*Grus grus*), as well as for barbary deer (*Cervus elaphus barbarus*), which has a limited distribution in North-African wood-pastures (Berrahmouni et al. 2009).

Drivers and consequences of recent changes to wood-pasture management

Traditionally managed wood-pastures are indeed excellent examples of sustainable land-uses, combining the generation of economic value under multiple management regimes and the maintenance of spatially heterogeneous and biodiversity-rich habitats (Spitzer et al. 2008; Hartel et al. 2015). However, these unique landscapes are increasingly reported to be undergoing a transformation throughout Europe to either oversimplified open pastures, or to closed-canopy forests and shrublands resulting from the lack of management (Pinto-Correia and Godinho 2013; Bergmeier and Roellig 2014; Kuemmerle et al. 2016). Several policy-dependent socio-economic triggers drive these contrasting land-use trajectories of intensification and land abandonment (Gómez-Baggethun et al. 2010; Fragoso et al. 2011).

Regular grazing as well as low-intensity exploitation are important for wood-pastures to maintain their characteristic semi-open and heterogeneous landscape features (Almeida et al. 2015). Low-intensity grazing has been widely shown to contribute towards herbaceous plant diversity and to facilitate the regeneration of shrubs and trees in wood-pastures (Aavik et al. 2008; Uytvanck van and Verheyen 2014). On the other hand, overgrazing by high livestock densities, or intense mechanical removal of shrubs, are reported to hamper tree and shrub regeneration in wood-pastures (Plieninger et al. 2004; Plieninger 2006; Arosa et al. 2015). The main triggers of grazing intensification include policy changes, such as the provision of higher subsidies for cattle raising (Pinto-Correia and Godinho 2013; Almeida et al. 2015). Additionally, the increasing pressure for food production associated with human population growth and fluctuations in the market values of wood-pastures products due to the demand for specific products (e.g. olive oil, early season fruits) have promoted the enlargement of specialized mono-culture croplands where chemical fertilizers are used more intensively (Stoate et al. 2009). Overgrazing and over-harvesting of crops, acorns and firewood are common in North Africa, also due

to pressures associated with the human population increase in Morocco, Algeria, and Tunisia (Berrahmouni et al. 2007; Campos et al. 2007; Bugalho et al. 2011a). In cork oak dominated areas, poor cork harvesting techniques, often related to the low wages paid to harvesters, also induce tree mortality (Bugalho et al. 2009).

The abandonment of wood-pastures has become widespread in some regions of Europe (Kuemmerle et al. 2016), often leading to an extreme reduction in grazing activity or even a complete ceasing of all land-use practices (Cramer et al., 2008; Estel et al. 2015). This is particularly common in isolated mountainous regions or areas with infertile soil, water limitations or harsh climatic conditions that greatly restrict grazing and agriculture efficiency (MacDonald et al. 2000; Rutherford et al. 2008). The lack of subsidies to support management activities can also contribute to lower land-use intensity, as it is the case in abandoned wood-pastures in Germany and in Estonia (Roellig et al. 2016; Roellig et al. 2018). In addition, insufficient subsidies for farming activities often lead to a decoupling of incentives from production outcomes, particularly in low-income farms, which can also lead to land abandonment (Stoate et al. 2009; Beilin et al. 2014; Terres et al. 2015). As a consequence of grazing abandonment, shrub regeneration and growth are leading to an increasingly developed understory cover in many landscapes (Castro and Freitas 2009). Together with a dense tree layer, uncontrolled shrub growth transforms open wood-pastures into closed and densely vegetated habitats, causing loss of open areas and overall habitat heterogeneity (Peco et al. 2006; Oldén et al. 2017).

Over-utilization and land abandonment can often occur within the same region, influencing the habitat structure across vast wood-pasture landscapes (Sales-Baptista et al. 2015). The most common consequence of these land-use changes is a loss of the semi-open and heterogeneous vegetation structure in wood-pastures (Plieninger et al. 2015). Moreover, these contrasting land-use trajectories induce changes in soil structure such as soil temperature, moisture and nutrient composition (Stoate et

al. 2001; Schmidt et al. 2017) that may influence seed germination as well as competition dynamics among plant species, which may result in important changes in plant richness and composition (Peco et al. 2005; Zarovalli et al. 2007; Castro et al. 2010b).

Influences of land-use changes on biodiversity, ecosystem functioning and ecosystem services

As stated above, wood-pastures usually harbour a high level of biodiversity, mostly due to their mosaic vegetation structure providing a diversity of niches that can be used by a wide range of species (Bergmeier and Roellig 2014; Moreno et al. 2016). Therefore, land-use driven factors influencing vegetation cover, heterogeneity and canopy openness risk altering niche distribution and availability, which may induce substantial changes in the biodiversity of wood-pastures (Azul et al. 2011; Martins et al. 2014; Ross et al. 2017). The effects of management type and intensity on biodiversity have long been a focus of research, particularly in human-shaped habitats (Flynn et al. 2009; Newbold et al. 2015). Negative impacts on species diversity associated with land-use intensification have been widely reported mostly due to decreases in feeding and nesting resources and habitat connectivity (Stoate et al. 2001; Kisel et al. 2011; Jeliazkov et al. 2016; Gossner et al., 2016). In fact, a recent review showed that overuse and intensive agriculture are the key drivers of biodiversity loss worldwide (Maxwell et al. 2016). On the other hand, the long-term absence of grazing results in a denser vegetation layer which has been shown to drive differences in species composition due to the loss of open habitat specialists (Russo 2007; Nikolov et al. 2011). Furthermore, changes in management intensity may also alter prey-predator relations and consequently the population dynamics of several species (Schekkerman 2008).

However, research has also underlined the existence of contrasting species responses to specific land-use strategies (Suarez-Seoane et al. 2002). For instance, Sebek et al. (2015) and Horák et al. (2018a)

showed that fungi and epigeic beetles have higher species richness in closed forests emerging from long-term land-abandonment where they benefit from humid conditions, whereas species richness of saproxylic beetles and reptiles decrease in these habitats due to the loss of open ground availability. Land use changes may alter various environmental factors simultaneously in the same habitat, such as dead wood quantity, understory density or soil temperature (Stoate et al. 2001; Castro et al. 2010a; Castro et al. 2010b), thus leading to contrasting species responses which ultimately depend on their various niche requirements. Exploring multi-taxa biodiversity patterns is therefore essential to provide a comprehensive understanding of the consequences of land-use changes, in addition to valuable insights on how to manage habitat conditions to ensure niche availability for wide range of species (Spitzer et al. 2008; Fournier et al. 2015; Pinho et al. 2016).

Furthermore, given that species responses to land-use changes are often driven by their specific ecological requirements, it is important to explore biodiversity patterns beyond the simple taxonomic patterns of communities (Jarzyna and Jetz 2016). For example, farmland birds such as *Falco naumanni* and *Tetrax tetrax* may benefit from the presence of agricultural fields (Franco and Sutherland, 2004; Silva et al. 2004), and replace species such as *Sylvia atricapilla* and *Troglodytes troglodytes* which are likely going to be absent from these areas due to the low availability of shrubs and trees (Godinho and Rabaça 2011). Thus, even if taxonomic diversity patterns remain somewhat stable in response to changes in land-use, there may be important changes in the ecological characteristics of local communities (Devictor et al. 2010). The concept of biodiversity represents the variation within species, among species and ecosystems, including the diversity of ecological processes that link species to ecosystems (Purvis and Hector 2000). There is a diverse range of terms used to refer to groups of species with similar ecological characteristics (i.e. the life history characteristics), including guild, functional group and functional type (Blaum et al. 2009). These terms usually represent groups of

species sharing morphological (e.g. body size, specific leaf area), physiological (e.g. photosynthetic pathway) or behavioural (e.g. foraging behaviour) features. Such features, usually referred to as traits or functional traits, are indicative of the multiple ecological functions and requirements associated with each species and can be used to identify niche in relation to environmental factors and other species in the ecosystem (Calow 1987; Petchy and Gaston 2006).

Some functional traits may reflect the capacity of species to respond to environmental changes; these are often referred to as response traits (Lavorel and Garnier 2002; Hooper et al. 2005). To illustrate, variations in specific leaf area of plants responding to increasing water stress may show us how sensitive the particular forest compositions are to drought (Greenwood et al. 2017). The dispersal ability of butterflies can also be considered a response trait as it plays a determinant role in the presence of butterfly species in fragmented habitats (Schtickzelle et al. 2006). However, traits may also show how species influence the habitat, i.e. effect traits, determining their contribution to ecosystem services such as nutrient cycling or seed dispersal (Hooper et al. 2005; Cadotte et al. 2011). For instance, the specific leaf area of plants can also affect their nutrient cycling capacity, and the dispersal ability of invertebrates influence the seed dispersal efficiency in relation to food provision service (Hevia et al. 2016). Variations in effect traits drive the mechanisms underpinning ecosystem service provision and can unravel how species functions on the ecosystem change along environmental gradients (de Bello et al. 2010). Some traits determine both species responses to the environment and their effects on ecosystem functions, and are simultaneously considered response and effects traits, but that is not always the case (Díaz et al. 2007). Consequently, trait choice is of crucial importance to the analysis of functional diversity and the selected traits must be closely associated to the environmental factors or ecological processes to be explored (Zhu et al. 2017).

Functional traits can help to reveal the complex relations between species and ecosystem services and two major hypotheses have been proposed to explain ecosystem processes in relation to community trait composition: the mass-ratio hypothesis (Grime 1998; Garnier et al. 2004) and the niche complementarity hypothesis mechanisms (Tilman et al. 1997). The mass-ratio hypothesis states that abundant species are the major driver of ecological processes in an ecosystem and the traits associated with dominant species will be the key drivers of ecosystem functions and services in the habitat (Grime 1998). The niche complementarity hypothesis postulates that a higher functional diversity of life history strategies in a community is associated with the existence of divergent traits which allow species to occupy the range of niches available in the habitat, thereby enhancing resource use efficiency, ecosystem functioning and services (Loreau 1998; Loreau 2000).

Functional diversity research has greatly expanded in recent years (Laureto et al. 2015), in large part due to the increasing availability of open trait databases, protocols for trait measurements (Blaum et al. 2009; Moretti et al. 2017) and the development of various analytical indices that can be used to reveal different aspects of functional diversity (e.g. functional richness, evenness and dissimilarity) and composition (e.g. community weighted means) (Mason et al. 2013; Plas van der et al. 2017). Combining these indices allows insights on both the overall diversity of traits and the relative abundance of individual traits present in a community, thus providing a holistic representation of the mechanisms underpinning the ecosystem functions and services (Dias et al. 2013). These indices can also be used to explore how functional traits vary along environmental gradients by measuring them for communities distributed under different environmental conditions (Mouillot et al. 2013).

There is a particular need to explore functional biodiversity in human-shaped habitats, where changes in land-use type and intensity are the key drivers of habitat conditions influencing the provision of multiple ecosystem services (Oppermann 2014; Laurila-Pant et al. 2015). Wood-pastures deliver a

range of important ecosystem services including the provision of food, fodder, timber and cork, the control of flood and soil erosion, climate regulation, the maintenance of diverse habitats for wide range of species, provision of pest and disease control as well as recreational areas and aesthetic value (Olea and San Miguel-Ayanz 2006; Moreno and Pulido 2009). Although ecosystem services are often only perceived by their delivery of values and goods for human well-being, the whole range of ecological processes associated with service provider and regulator species play a key role in the final provision of services to humans (Kremen 2005; Cardinale et al. 2012; Huber et al. 2013). For instance, canopy closure as a result of reduced management can lead to thinner bark development which influences the quality of bark, and consequently its market value (Eriksson 2008). Another example is the impact of management type on trait composition and functional diversity of wild bees, which in turn may influence pollination and ultimately the provision of food resources (Hall et al. 2019). Importantly, recent studies suggest that land-use changes may result in potential changes in the provision of several important ecosystem services provided by wood-pastures, such as pest control, seed dispersal, pollination or water provision, but such changes remain inadequately documented and tested (Moreno et al. 2018; Pantera et al. 2018).

Challenges in improving conservation efforts for wood-pastures

Maintaining both the economic and biodiversity values provided by wood-pastures is the main challenge for their long-term sustainability and a major focus of efforts to protect these social-ecological systems (Hartel and Plieninger 2014b). Besides several national policies developed to preserve these valuable ecosystems, they are also under the protection of European legislation, such as the EU Habitats Directive and the Common Agricultural Policy (CAP). These directives are the main legal instruments regulating the management and conservation of European habitats (Hartel et al. 2013; Beaufoy 2014). The EU Habitats Directive, along with the EU Birds Directive, aims to preserve

wildlife and natural European habitats by defining and protecting priority areas and species of conservation concern (European Union 1992). The Common Agricultural Policy (CAP), regulates agricultural production and provides subsidies for land managers to sustain active land management practices, including in wood-pastures, based on various criteria which define the land eligible for management support (Zanten van et al. 2014). However, there are several challenges regarding the regulations imposed by these legal instruments which create obstacles for sustainable management efforts aiming to balance economic and natural values in wood-pastures (Mosquera-Losada et al. 2018).

To begin with, the classification of European habitats considered in Annex I of EU Habitat Directive (European Commission 2013) includes four types of wood-pastures as "*Juniperus communis* formations on heaths or calcareous grasslands", "Mediterranean arborescent matorral", "Sclerophyllous grazed woodlands" and "Fennoscandian wooded pastures". The main limitation of this classification is that it partly or completely excludes several major wood-pasture types under various human-uses, such as deciduous wood-pastures in north-central and northern Europe, montane to subalpine pasture areas, macchia/matorral of *Quercetea ilicis* landscapes in the Mediterranean region, orchards with fruit-crop trees and groves with olive or carob trees (Bergmeier et al. 2010). Unclear definitions of what constitutes a wood-pasture in these main policies leads to the inadequate conservation status of these habitats (Peeters 2012; Jakobsson and Lindborg 2015). Moreover, this problem associated with an unclear definition of wood-pastures interlinks with CAP subsidies and incentives for different land-uses, which should target all types of wood-pastures specifically in addition to pasture or forest dominated habitats, rather than focusing on either pasture management or forest regrowth (Molnár et al. 2016; Erdős et al. 2018b). This ends up contributing to distort the semi-open structure of wood-pastures and inducing overuse and land abandonment as outlined above.

To mitigate these stated problems, several alternative schemes have been established to stimulate sustainable management in wood-pastures. Agri-Environment schemes (de Snoo et al. 2013) associated to the High Nature Value (HNV) concept (Andersen et al. 2003) direct managers to non-intensive and biodiversity-friendly farming practices and propose the implementation of conservation plans in areas where agriculture is the main management activity. The HNV concept also aims to preserve specific landscape elements such as hedges, ponds, rocky outcrops and riparian vegetation that contribute to the spatial heterogeneity of wood-pastures and thereby help maintain their high biodiversity value (Ferraz-de-Oliveira et al. 2016). Another relevant effort is the Forest Stewardship Council (FSC) certification scheme that certifies forestry products and managers based on environment-friendly land-use criteria to promote both nature conservation and economic returns. FSC certification efforts address sustainable forest management by aiming to preserve and promote the market value of timber as well as non-timber forestry products (Auld et al. 2008) in order to reduce the harvesting pressure. Aiming to prevent extensive land abandonment, the "less-favoured areas" (LFA) scheme, which is part of EU's Rural Development Policy, aims to provide incentives to sustain management in areas prone to abandonment due to social or natural constraints (Dax 2005). Finally, there is an increasing effort to establish payment for ecosystem services (PES) programmes to supports managers who contribute to ecosystem service provision through non-intensive management strategies favouring biodiversity conservation (Wunder et al. 2008).

Several studies have reported that most of these efforts, along with several other schemes (Plieninger et al. 2015), have contributed to maintain or enhance spatial heterogeneity and biodiversity in wood-pastures (Bugalho et al. 2011a). However, to sustain these positive consequences in the long-term and to provide new insights to improve sustainable management efforts, there is a need for contributions from the scientific community revealing how land-use driven changes and conservation efforts

influence biodiversity patterns in wood-pastures, and inform managers and policy makers on land-use practices integrating economic and natural values (Rey Benayas et al. 2008; Lindenmayer et al. 2008; Roellig et al. 2016; Kuemmerle et al. 2016). For example, a recent study showed how previous CAP criteria establishing a limit for the number of trees per hectare to define eligible land for support, had a negative influence on the biodiversity of wood-pastures (Jakobsson and Lindborg 2015).

Furthermore, Rolo et al. (2016) explained how both production and biodiversity conservation can be promoted by exploring the optimum woody vegetation cover that ensures high biodiversity value in wood-pastures without need of extensive land sparing from the pasture component. In addition, (Morandin et al. 2014) suggest that managing abandoned hedgerows may enhance food and fodder provision, increase the availability of refuge habitats for several species, and substantially contribute to natural pest control, thus reducing the need for expensive and detrimental chemical use in cropped wood-pastures.

In summary, searching the ways of sustainably engaging human-use in conservation plans is needed to provide new strategies to maintain productive and biodiversity-rich social-ecological systems (Fischer et al. 2008; Tscharntke et al. 2012; Leal et al. 2018).

Main aims and outline of the thesis

The overall objective of the thesis is to explore taxonomic and functional diversity patterns of multi-taxa across habitat conditions associated with different management strategies throughout Iberian and North African wood-pastures. This work proposed to reveal species and trait level variations in plant, lichen, beetle and bird communities to understand the factors driving biodiversity and ecosystem functioning and services in relation to land-use changes. The final aim of this thesis is to provide insights on biodiversity-friendly and sustainable management actions that can contribute to conciliate

the natural and economic values of wood-pastures. The thesis is comprised of four interlinked studies whose specific aims and methodological approaches are summarized below.

Chapter 2. Increasing biodiversity in wood-pastures by protecting small shrubby patches

This chapter focuses on the biodiversity contribution of small shrubby patches within the wood-pasture matrix by evaluating the impact of these patches on species composition and species richness patterns of multi-taxa. Specifically, species assemblages of plants, lichens and coleopterans were sampled in small shrubby patches (252 to 3000 m^2) and in plots in the adjacent wood-pasture matrix in two Portuguese *montado* areas. The analysis explored the differences in species composition between the shrubby patches and the matrix and quantified the contribution of the patches to the overall species richness of wood-pastures at the local-scale.

Chapter 3. The contribution of small shrubby patches to the functional diversity of wood-pastures

This study aimed to investigate trait-level diversity of shrubby patches and the matrix habitat of small-scale wood-pastures of Portugal (*montados*). We explored the functional composition (community weighted means) and functional diversity (functional dispersion and functional evenness) patterns of plants, coleopterans and lichens comparing small shrubby patches (252 to 3000 m^2) and plots in the wood-pasture matrix. The analyses are based on functional diversity approaches to characterize the functional structure of shrubby patches and the adjacent matrix and reveal the functional diversity of multi-taxa.

Chapter 4. Bird taxonomic and functional responses to decreasing management intensity in wood-pastures

This chapter explored how changes in habitat structure associated with a management intensity gradient ranging from active management towards land abandonment, affect bird taxonomic diversity, functional diversity and trait assemblages across wood-pastures in Iberian Peninsula and North Africa. Bird assemblages were sampled in thirty-seven wood-pastures throughout Portugal, Spain and Morocco during the breeding season and habitat variables were collected at the same locations. The analysis focused on exploring the influence of changes in habitat structure on species richness, Shannon diversity, functional diversity and functional composition of breeding birds.

Chapter 5. Wood-pasture abandonment leads to a reduction of insectivore bird functional diversity with potential consequences for pest control

Chapter 5 assesses the influence of a management intensity ranging from active management to land abandonment on the taxonomic and functional diversity of insectivore birds in Iberian and North African wood-pastures. This study aimed to answer whether the taxonomic and functional diversity of insectivorous birds responds to changes in habitat structure linked to management intensity and how effect traits associated with pest regulation vary in relation to these changes in the habitat.

Finally, Chapter 6 highlights the main findings of the thesis, proposes a set of management actions that could enhance the biodiversity of wood-pastures, discusses some limitations of the presented studies and outlines future research directions.

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CHAPTER 2

Increasing biodiversity in wood-pastures by protecting small shrubby patches

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Abstract

Wood-pastures are grazed systems, widespread across Europe, where natural and economic values often co-exist. Social and economic changes in Europe generate both threats and opportunities to these systems, calling for new or improved management strategies. We studied the potential of increasing the biodiversity of wood-pastures through the promotion of small-scale habitat diversification. More specifically, we evaluated the impact of protecting very small shrubby patches within large Mediterranean wood-pastures. We sampled species assemblages of plants, lichens and coleopterans in 13 small patches (252 to 3000 m^2) with a well developed shrub layer, and 11 plots in the adjacent matrix of virtually shrub free wood-pasture. Despite their very small size, patches had clearly distinct assemblages of all the studied taxa and their presence greatly enhanced the species richness of the studied wood-pasture landscapes. The presence of shrubby patches increased species richness in wood-pastures by 42% for plants, 27% for lichens and 29% for coleopterans (average over two study areas), a very substantial gain considering that patches covered less than 0.5% of the studied wood-pastures. Our results indicate that the protection and promotion of even small shrubby patches is a promising low-cost nature-based strategy to increase the biodiversity value of wood-pasture landscapes, without substantially affecting the economic value of this silvopastoral system, which is an old and important part of the natural and cultural heritage of Europe.

Keywords: species diversity; habitat management; montado/dehesa; multi-taxa; native vegetation; silvopasture

1. Introduction

The massive conversion of natural habitats to production land is the single most important threat to the world's biodiversity (Gonthier et al., 2014; Maxwell et al., 2016; Gossner et al., 2016; Lanz et al., 2018), and conservationists have realized that setting aside samples of the original habitats in protected areas is insufficient to preserve it (Rands et al., 2010; Fischer et al., 2014; Kremen, 2015). This explains ongoing efforts to develop strategies making production landscapes more biodiversity friendly, i.e. adequate to host significant levels of biodiversity and allowing connectivity among protected areas. Finding ways to improve the biodiversity value of these landscapes, without compromising their economic productivity is thus an important challenge for conservation ecology (Mönkkönen et al., 2014). One of the most important potential drivers of biodiversity loss in production landscapes dominated by forestry or agriculture is a decline in habitat diversity (Hendrickx et al., 2007; Alsterberg et al., 2017). To counter this problem and promote biodiversity rich landscapes, it is imperative to develop management strategies that increase compositional landscape heterogeneity (Gámez-Virués et al., 2015).

Wood-pastures, also known as pasture-woodlands, are systems usually dominated by grasslands and a variable density of trees which cover vast areas in the temperate zones, including in Europe (Plieninger et al., 2015). The concept of wood-pasture includes a broad range of botanically distinct, but structurally similar, semi-natural systems (Bergmeier and Roellig, 2014). Their capacity to host biodiversity is usually high (Diaz et al., 1997; Hartel and Plieninger, 2014; Simonson et al., 2018) but in some regions may be constrained by a lack of spatial habitat heterogeneity. In fact, while in some areas wood-pastures are interspersed with other types of land use or landscape elements (Bergmeier and Roellig, 2014), there are vast areas where intensification and economies of scale over the centuries led to reduced spatial heterogeneity.

It has been demonstrated that habitat heterogeneity resulting from the presence of, for example, even small stretches of riparian vegetation can substantially improve the overall biodiversity wealth of the wood-pasture landscapes (Leal et al., 2011; Rosalino et al., 2009; Silva et al., 2011). Consequently, promoting riparian vegetation in these landscapes is a positive management intervention (Leal et al., 2016), but the potential of this strategy may be limited by the availability of suitable valleys and watercourses. There is thus a need to find additional management strategies to increase habitat heterogeneity and connectivity within wood-pastures, without causing a significant loss of economic value. Wood-pastures are often created by the tree thinning and artificial elimination of the shrub layer of the original woodland, reducing the system to its herb and tree layers, to increase grazing carrying capacity (Listopad et al., 2018). We hypothesized that preventing the elimination of this shrub layer and allowing the regeneration of native vegetation, even in very small patches, would promote the diversity and complexity of the habitat sufficiently to increase the biodiversity wealth of wood-pastures.

The potential of increasing heterogeneity by simply allowing the establishment of small patches of native shrubs is substantial, because this measure adds a functional layer usually absent in the matrix of grazed wood-pasture (henceforth referred to as “matrix”). Moreover, shrubs have an important role in supporting tree regeneration (Callaway, 1992; Van Uytvanck et al., 2008; Pulido et al. 2010) and thereby contributing substantially to the succession of the mosaic vegetation structure in wood-pastures (Olff et al., 1999; Vera et al., 2006; Van Uytvanck and Verheyen, 2014). Thus, as time passes, the vegetation in the patches is likely to acquire a structure and floristic composition that is much closer to that of the ancestral forest type than the matrix, creating conditions to support additional native species of a variety of taxonomic groups. Finally, the denser vegetation may create microclimatic conditions that are substantially different from those in the matrix (Cuesta et al., 2010), moderating limiting factors such as dryness and extreme temperatures that can have adverse impacts on local communities (Príncipe et al., 2014; Correia et al., 2015). The presence of marginal habitats, such as shrub

encroached pastures, olive-fruit orchards and water streams, has been shown to contribute to habitat heterogeneity and increase the species diversity of plants, spiders, bees and earthworms in wood-pastures (Moreno et al., 2016) but they may also benefit several other biological groups and thus make a significant contribution to wood-pasture biodiversity. Promoting a strategy that stimulates habitat heterogeneity and enhances biodiversity by allowing small patches of diverse habitats to develop in wood-pastures would be akin to the Woodland Key Habitats (WKH) concept, which involves the protection of small patches of habitat within a matrix of production boreal forest. The WKH concept tends to focus on slightly larger habitat patches than those discussed here for wood-pastures and its implementation varies from country to country but, despite some shortcomings, this approach has resulted in positive impacts for biodiversity (Timonen et al., 2011).

One of the types of wood-pasture that may benefit from the proposed management measure are the vast "montados" or "dehesas" that cover extensive areas in both the European and African sides of the western Mediterranean basin. They usually have a tree layer dominated by native oak trees (*Quercus rotundifolia, Q. suber* and *Q. pyrenaica)* and hold a rich biodiversity alongside an important economic value. They are recognized as High Nature Value (HNV) farmland and are focus of conservation measures under the European Union Habitats Directive (European Union, 1992). Socio-economic changes are driving various factors that threaten this ecosystem in much of its range (Bugalho et al., 2011a).

The overall objective of this paper is to contribute to the development of strategies to increase the biodiversity value of wood-pastures by investigating the effects of small-scale habitat diversification. More specifically, using Mediterranean oak wood-pastures as a model system, we evaluated the impact on biodiversity of protecting very small shrubby patches within large areas of wood-pasture. As model taxa we used plants, lichens and coleopterans, which were selected due to their different ecological roles. For example, plants are central in the definition of the structure of the

ecosystem and are strongly influenced by grazing and management (Diaz et al., 2007). Lichens reflect the interface between the atmosphere and the substrate, are regarded as good indicators of ecosystem condition and respond to changes in grazing intensity (Pinho et al., 2012). Coleopterans are a speciose group of arthropods comprised of species with different foraging requirements and are sensitive to grazing (Kruess and Tscharntke, 2002). We first determined how the species assemblages of these small patches, surrounded by wood-pasture, differ from those of the matrix. Then we quantified the impact of the presence of the patches on the richness of the model taxonomic groups at landscape level.

2. Materials and Methods

2.1. Study Area

Sampling was conducted during 2012-2013 and replicated at two nearby areas in southern Portugal, Freixo do Meio (38º 42'N, 8 º 19.1'W) and Barrocal dos Ricos (38º 46'N, 8 º 15'W), located about 10 km from each other (Figure 1). The region has a Mediterranean climate, with hot and dry summers (Köppen Climate Classification = Csa, Agencia Estatal de Meteorología, Instituto de Meteorología, 2011). Both areas are dominated by cork (*Quercus suber*) and holm oak (*Q. rotundifolia*) "montado" wood-pastures, used for livestock grazing (cattle, sheep and pig), cork extraction and hunting. Shrub encroachment is usually avoided using mechanical removal and grazing but in both study areas there are small patches where shrubs have been allowed to grow. These are usually associated to small rock outcrops in which shrubs can grow because the rocks prevent mechanical clearing. The vegetation of these patches usually includes a variable number of the same trees that dominate the surrounding wood-pasture, and a more or less developed shrub layer composed by native species like *Cistus* spp., *Quercus* spp., *Pistacia lentiscus*, *Olea* spp. and *Arbutus unedo*.

In Freixo do Meio we identified and sampled nine of these shrubby patches (henceforth

"patches") and seven nearby sites within the grazed wood-pasture matrix with few shrubs, as typical of these wood-pastures when managed. In Barrocal dos Ricos we sampled four shrubby patches and four plots in the nearby matrix. A total of 24 sites were thus sampled (13 shrubby and 11 matrix). In both study areas we sampled all the available patches with well-developed shrubs that covered at least 250 m^2. The matrix of wood-pasture around the patches, where we selected the matrix sampling plots, is quite flat and homogeneous. All matrix plots were selected haphazardly within the same block of wood-pasture of the shrubby patches, or in immediately adjacent blocks. They were all at least 140 m away from the nearest shrubby patch, at least 100 m from each other, and not close to edges, roads, buildings, livestock watering stations and drainage lines. The area sampled in each matrix plot varied across the three taxa, as explained bellow. In both study areas all sampled sites are located within a radius of less than 1 km. Each shrubby patch was characterized using the following parameters: patch area, proportion of ground covered by exposed rocks (on a scale of 0 to 5), height of the understory, height of the trees, density of vegetation on a scale of 1 to 10 and the available tree species (Table S1). Due to management, the plots sampled in the matrix were much less variable than the shrubby patches; tree density was quite homogeneous at about 30 trees/ha (cork or holm oaks) and shrub and rock cover was minimal. The number of matrix plots and patches is not the same because some of those that were sampled had to be excluded from the analysis because pigs and wild boars repeatedly interfered with pitfall traps.

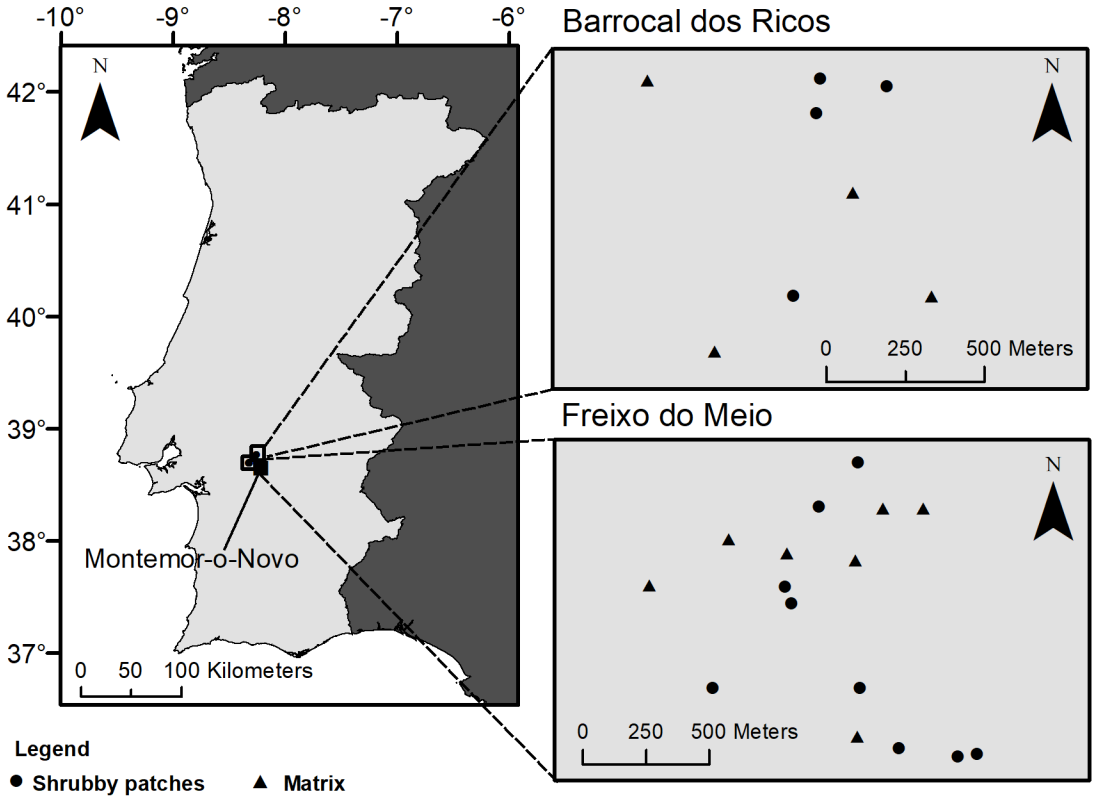


Fig. 1. Location of the study areas, Barrocal dos Ricos and Freixo do Meio (Montemor-o-Novo, Portugal). Circles represent sampled shrubby patches and triangles sites sampled in the wood-pasture matrix.

Table 1

Characteristics of sampled shrubby patches in Freixo do Meio and Barrocal dos Ricos; patch area (m^2), proportion of ground covered by exposed rocks (on a scale from 0 to 5), height of the understory (m), height of the trees (m), index of plant density on a scale of 1 to 10 and species of trees.

Sites	Patches	Patch size (m^2)	Index of rock cover	Height of the understory (m)	Height of the trees (m)	Index of plant density	Species of trees
Freixo do Meio	**P1**	927	3	3	6	9	*Q. rotundifolia* *Q. coccifera* *P. lentiscus*
	P2	607	2	5	8	9	*Q. rotundifolia* *Q. suber*
	P3	579	1	6	8	7	*Q. rotundifolia* *Q. suber* *P. lentiscus*
	P4	1009	1	5	7	8	*Q. rotundifolia* *Q. suber* *O. europaea* *Q. coccifera* *P. lentiscus*
	P5	3000	0	3	5	5	*Q. rotundifolia* *Q. suber* *Q. coccifera* *P. lentiscus*
	P6	2500	0	1	5	5	*Q. rotundifolia*
	P7	252	0	5	6	10	*Q. coccifera*
	P8	402	0	5	8	10	*Q. rotundifolia* *P. lentiscus*
	P9	1195	1	5	8	8	*Q. rotundifolia* *P. lentiscus*
Barrocal dos Ricos	**P10**	1520	1	3	6	8	*Q. rotundifolia* *O. europaea*
	P11	889	1	3	6	7	*Q. rotundifolia* *O. europaea*
	P12	1044	1	3	5	7	*Q. rotundifolia* *O. europaea*
	P13	2015	2	2	5	7	*Q. rotundifolia* *O. europaea*

2.2. Sampling of species assemblages

The assemblages of plants, lichens and coleopterans were sampled in all shrubby patches and matrix plots by experts in each taxonomic group during 2013-2014. In this study we analysed presence-absence information for all taxa (Table S2). Shrubs, grasses and forbs were surveyed in 10x10m quadrats, always by the same observer between May and July 2013. In each shrubby patch, a quadrat was placed with one of the sides along the edge of the patch but clearly inside the patch. Quadrats were placed close to the edges because the small size and dense vegetation in some shrubby patches often prevented quadrats to be placed deeper inside the patch. In the habitat matrix quadrats were also 10 x 10 m and all included areas with and without canopy cover. Plant species present in each quadrat were identified in the field or in the laboratory, and they were recorded using the Braun-Blanquet scale (Kent and Coker, 1996).

Lichen sampling was carried out between December 2013 and January 2014. To survey lichens in shrubby patches, we first sampled the trunks of all cork oaks (*Quercus suber*) and holm oaks (*Quercus rotundifolia*) in the patch with a diameter at breast height (dbh) larger than 15 cm (always fewer than five). Following the European standard protocol (Asta et al., 2002), a 10x50 cm frame divided into five 10x10cm grid-cells was vertically placed over each tree trunk at about 1 m above the ground. This process was repeated in four different orientations (N, S, E, W). Each survey was then complemented by a two-hour long search for lichens on other species of trees (if any present), on rocks and on the ground. The procedure to survey the lichens in matrix plots was the same, but here we sampled a fixed number of five trees per plot. Each lichen species occurring inside each grid cell was recorded and all but three species recorded were identified to species level in the field or in the laboratory. The same observer carried out the lichen sampling in all sites.

Coleopterans were sampled with pitfall traps during late May and June 2013. These traps capture a broad variety of arthropods but are particularly efficient for epigeal species. Each trap was a

polystyrene cup with a 95 mm diameter, sunk in the soil with the rim flush with the soil surface, and filled with about 3 cm of water with soap and salt. Three traps were placed in each patch and matrix plot; the location of the first trap was chosen haphazardly and the other two traps were placed about 10 m from this first trap and from each other in a triangle shape. They remained in the field for five weeks, but the captured arthropods were removed each week and preserved in 70% alcohol with glycerine. Captures in the same patch or matrix site were pooled before analyses. All but nine Coleoptera were identified to species level.

2.3. Data Analysis

To determine if the species assemblages of shrubby patches were consistently different from those of the adjacent wood-pasture matrix, we used correspondence analysis (CA) based on chi-square distance. First, we performed two ordinations by pooling all species separately for the two study areas - Freixo do Meio and Barrocal dos Ricos. Later, we also performed a CA for each taxon separately in the two study areas. We then used a non-parametric permutation test of significance (ANOSIM) using Bray-Curtis distance for each taxon to determine the statistical significance of the differences between the assemblages of shrubby patches and the wood-pasture matrix. Separate analyses were done for the two study areas, Freixo do Meio and Barrocal dos Ricos, to have a replicate for the effect of the patches and to minimize the risk of confounding the results with any undetected differences between the areas. These analyses were performed in R (R Core Team, 2016) using the packages “ca” (Nenadic and Greenacre 2007), “factoextra” (Kassambara and Mundt, 2017), “vegan” (Oksanen et al., 2016) and “ggplot2” (Wickham, 2016).

To assess the influence of the presence of shrubby patches on the overall richness of the landscape, we compared the richness of wood-pastures with and without shrubby patches, using sample-based rarefaction analysis (Chao et al., 2014). To do this, for each of the study sites we

generated two rarefaction curves: one including only the sites sampled in the matrix (7 sites for Freixo do Meio and 4 sites for Barrocal dos Ricos) and a second that included both the sites in matrix and in shrubby patches (16 sites for Freixo do Meio, 8 sites for Barrocal dos Ricos). The number of sites used to generate the latter curve was larger, but we truncated it to make the comparison at 7 rarefied richness for Freixo do Meio and 4 rarefied richness value for Barrocal dos Ricos. Analyses were done separately for each of the model taxon and study areas, using "iNEXT" (Hsieh et al., 2016) R package. Finally, for each taxa we run a random effects generic inverse variance meta-analysis to test for differences in richness between matrix alone and matrix with patches, combining the probabilities of the two study areas, using the R package "meta" (Schwarzer, 2007).

We also tested whether the spatial distance between sampling sites had any effects on species richness using a Mantel test (Mantel, 1967; Sokal, 1979) implemented with "ade4" package (Bougeard and Dray, 2018) but no statistically significant ($p>0.05$) spatial effects were detected.

Although not all shrubby patches have rocks covering part of the ground, most of them do. A few have well developed rock outcrops but most have just a few rocks or even no rocks above the ground surface (Table S1). The plots sampled in the wood-pasture matrix had only a few rocks. We tested if the effects of rock cover, patch type and study area influenced the richness of the species assemblages. This was done using a separate Generalized Linear Mixed Models (GLMMs) for each of the three model taxa. We modelled rock cover (in classes ranging between 0 to 5) and patch type (shrubby patch or matrix plot) as fixed effects and study areas (FM or BR) as a random effect using restricted maximum likelihood method (REML). These analyses were performed using "lme4" package (Bates et al., 2015) and "lmerTest" package (Kuznetsova et al., 2017) in R (R Core Team, 2016).

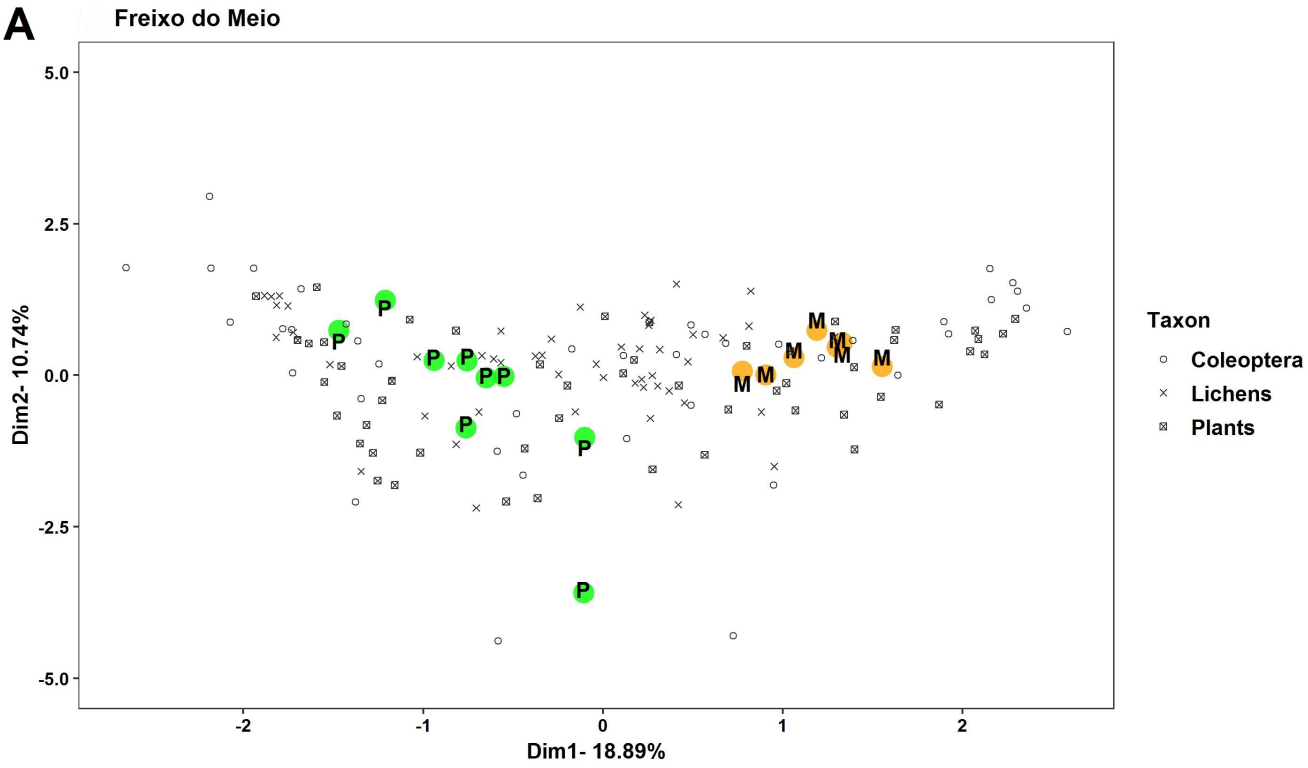
3. Results

The 13 shrubby patches that we identified, characterized and sampled were between 252 m^2 to 3000 m^2 (median value: 1009 m^2). Several characteristics of these patches (patch area, proportion of ground covered by exposed rocks (on a scale of 0 to 5), height of understory, height of trees,index of plant density on a scale of 1-10 and the available tree species are shown in Table S1. Our sampling allowed the identification in the two study areas of a total of 75 species of plants, 65 of lichens and 56 of Coleoptera.

3.1. Distinctiveness of species composition of assemblages in shrubby patches and matrix

The first axis of the CA ordination of the patches of Freixo do Meio explains 18.89% of the variation in species composition and clearly separates the assemblages of shrubby patches and of wood-pasture matrix (Figure 2A). The results for Barrocal dos Ricos were very similar, with the first axis of the CA ordination explaining 34.95% of the variance and contrasting the shrubby patches and the matrix (Figure 2B). Although shrubby patches have many species in common with the matrix, the ordinations of all taxa combined show that the distinctiveness of the species assemblages of the patches is very marked (Figure 2). It is worth noting that even the few patches that did not have exposed rocks on the ground in Freixo do Meio clearly cluster with the remaining shrubby patches, not with the matrix (Figure 2A). These results were corroborated by the CA carried out for each taxonomic group independently (Figure S1), which show clear differences in species composition between the shrubby patches and the matrix. This suggests that the differences in species composition between shrubby patches and the matrix revealed by the global CA ordination are not driven by a single group and reflect true differences in species composition across taxa.

The ANOSIM results (Table 2) show that species composition in shrubby patches and the matrix is clearly different. The strength of the differentiation, reflected in the R-statistics, was high in all the study taxa and in the two study areas.



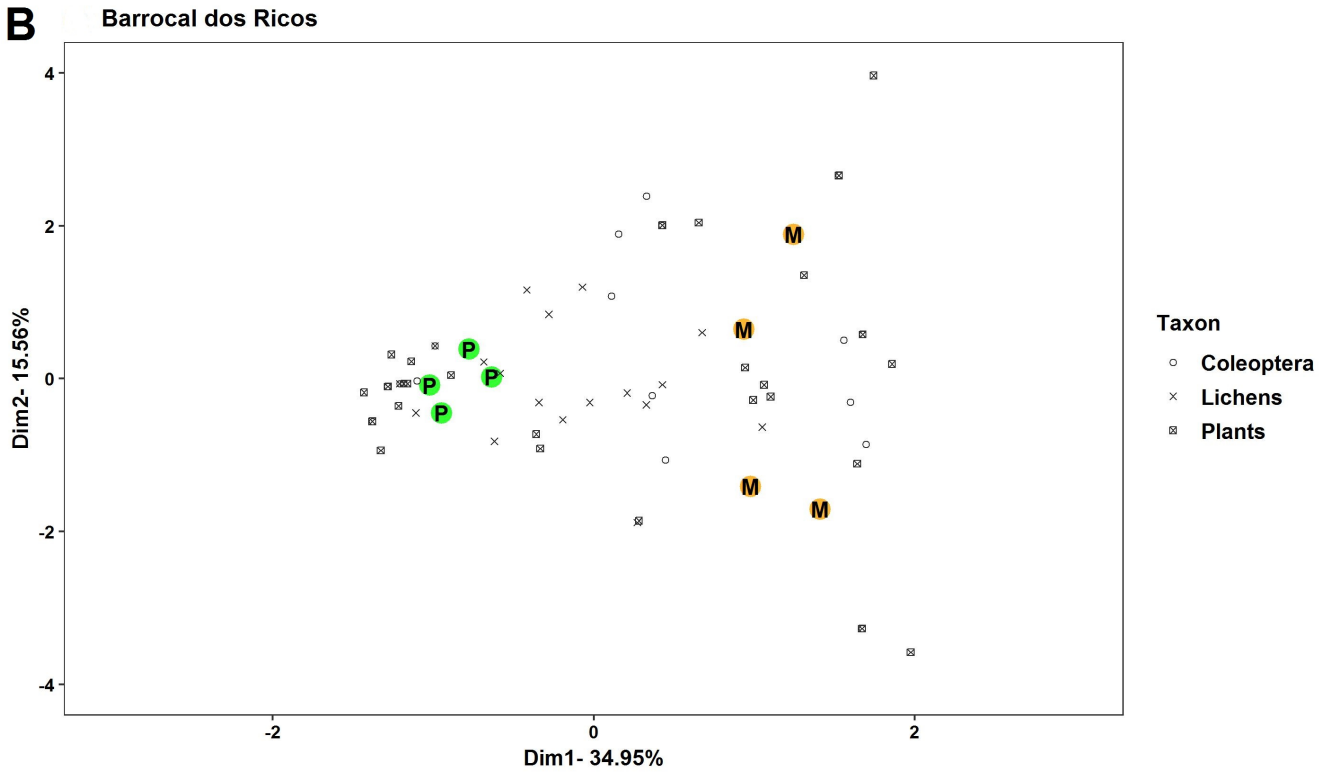
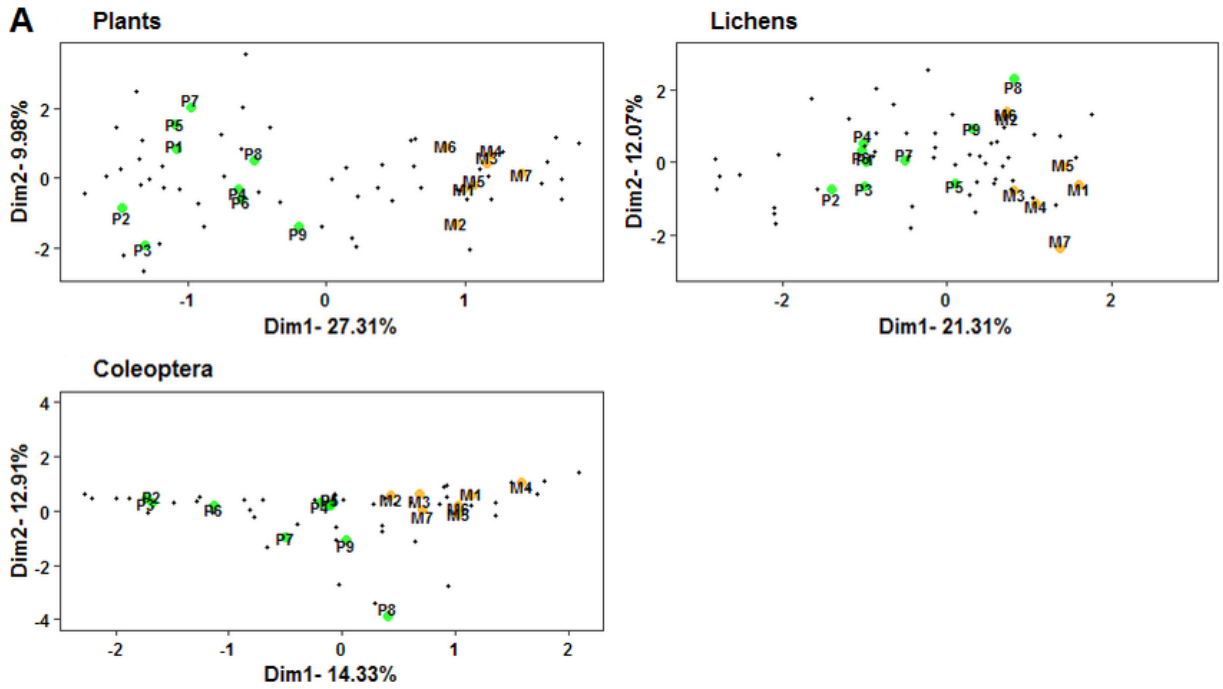


Fig. 2. Correspondence analysis (CA) ordination of the sampled sites in matrix and shrubby patches in the two study areas (**A)** Freixo do Meio and (**B)** Barrocal dos Ricos, using all species of the three studied taxa. In both cases the first axis clearly separates the patches (P) from the matrix (M).



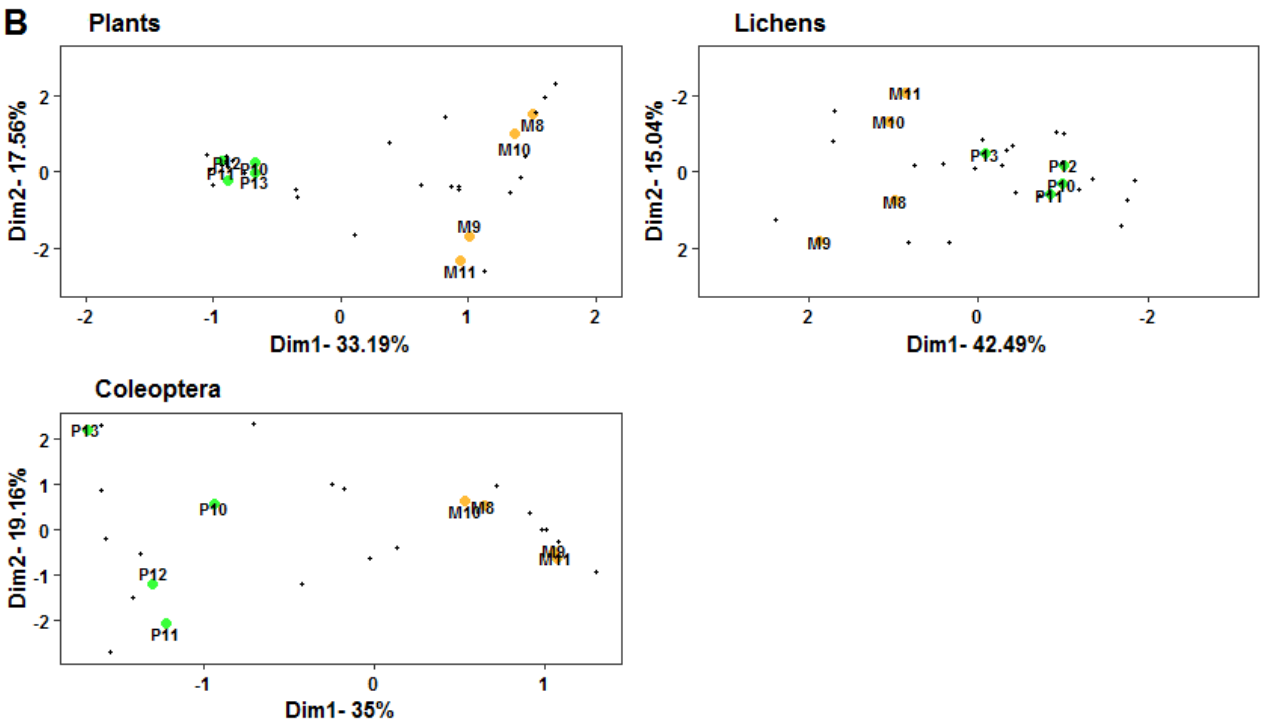


Fig. 3. Correspondence analysis (CA) results of the sampled sites in matrix (M) and patches (P) in (**A**) Freixo do Meio and in (**B**) Barrocal dos Ricos, analysing each taxon separately.

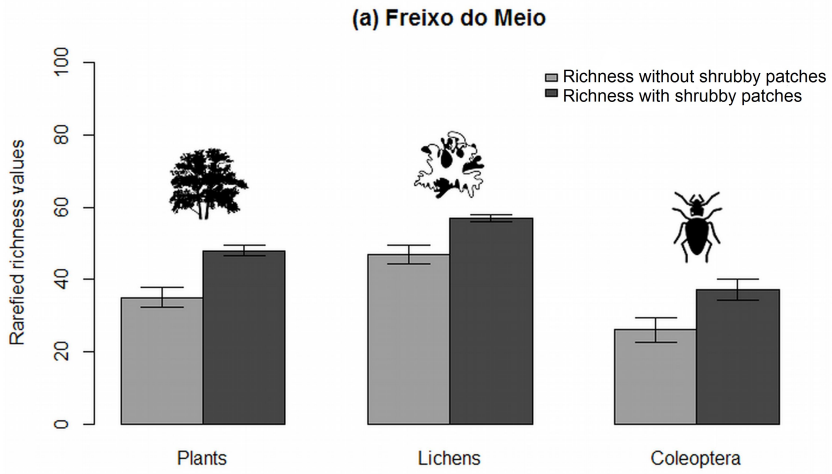
Table 2

Results of the Analysis of Similarities (ANOSIM) using Bray-Curtis distance, for the two wood-pasture areas (Freixo do Meio and Barrocal dos Ricos). Values of the R-statistics closer to 1 indicate a greater dissimilarity between the species assemblages of shrubby patches and the matrix. The p-values indicate the statistical significance of the difference.

Study areas	Plants	Lichens	Coleoptera
Freixo do Meio	R=0.901; *p=0.001*	R=0.45; *p=0.004*	R= 0.616; *p=0.003*
Barrocal dos Ricos	R= 0.920; *p= 0.003*	R=0.885; *p= 0.03*	R= 0.921; *p= 0.03*

3.2. Influence of shrubby patches on species richness

Figure 4 shows that, in our samples of the three taxa, the mean rarefied species richness in wood-pastures with shrubby patches was systematically higher than without them. Moreover, the 84% confidence intervals do not overlap in any taxa in Freixo do Meio, as well as in plants and lichens in Barrocal dos Ricos, indicating that most differences observed at each of the two areas are significant at the 0.05% level (Cumming and Finch, 2005; MacGregor-Fors and Payton, 2013). Finally, the meta-analysis testing the differences for the combination of the two areas shows that they are highly significant for plants and lichens ($p < 0.0001$) and significant for coleoptera ($p < 0.015$). These results demonstrate that, overall, the presence of shrubby patches substantially increased species richness in both study areas (Figure 4), although this difference is less evident for Barrocal dos Ricos where the number of sampled patches was lower. The gain in species richness was 42% for plants, 27% for lichens and 29% for Coleoptera (average for the two study areas).



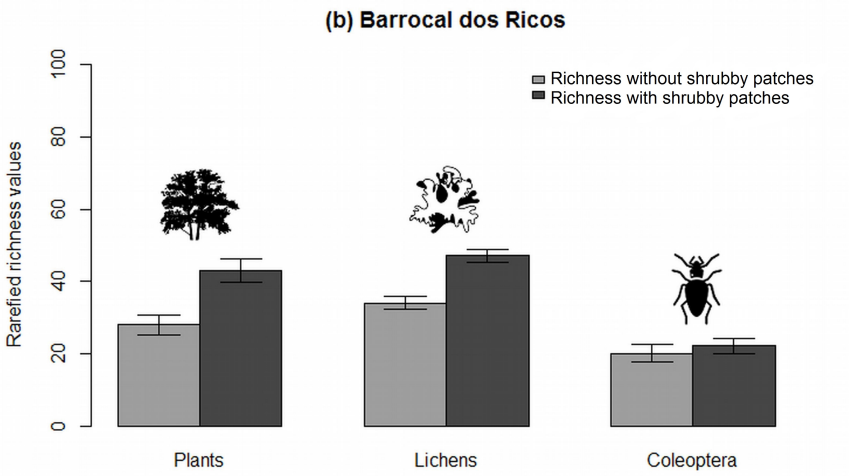


Fig. 4. Rarefied richness values in the two study areas (a) Freixo do Meio and (b) Barrocal dos Ricos with and without shrubby patches and respective 84% confidence intervals. It is evident that the presence of shrubby patches increases species richness substantially in Freixo do Meio for all taxa and in Barrocal dos Ricos for plants and lichens.

The results of the Generalized Linear Mixed Models (GLMMs) carried out to identify whether rock cover, patch type and study area influences species richness were not significant for plants and beetles (Table 3). Rock cover only had a positive effect on lichen species richness and there was no significant difference for patch type (Table 3).

Table 3

Summary table of Generalized Linear Mixed Models (GLMMs) results testing the influence of rock cover and patch type (fixed effects) and study area (random effect) on species richness of plants, lichens and coleopterans. The table shows the estimate, standard error (Std. Error), t value and *p*-value for fixed effects and the variance for the random effect returned by the models.

Fixed effects:				
Plants	**Estimate**	**Std. Error**	**t value**	***p*-value**
Intercept	17.3270	2.4557	7.056	0.021
Rock cover	-0.3732	2.0049	-0.186	0.854
Patch type	2.9945	3.2795	0.913	0.372
Lichens				
Intercept	24.696	3.689	6.695	0.065
Rock cover	3.923	1.705	2.300	**0.032**
Patch type	4.952	2.789	1.776	0.090
Coleopterans				
Intercept	9.9091	0.8564	11.570	1.42e-10
Rock cover	-1.2000	0.8982	-1.336	0.196
Patch type	0.2140	1.4700	0.146	0.886
Random effect:				
	Variance			
Plants Study area	4.673			
Lichens Study area	21.83			
Coleopterans Study area	0.000			

4. Discussion

4.1. Shrubby patches and wood-pasture matrix have distinct species composition

Our results show that even small shrubby patches, as small as 252 m^2, have species assemblages that are very distinct from those of the wood-pasture matrix. The most contrasting assemblage is that of plants (Table 2), which is unsurprising because the great majority of woody species that are part of the local natural vegetation are artificially repressed in wood-pastures. In fact, the ground vegetation layer of Mediterranean wood-pastures is usually rich in grasses and forbs, but woody species are scarce in intensively managed and grazed areas.

The shrubby patches with a floristically and structurally richer vegetation, has cascading impacts on a multitude of taxa, such as lichens and coleopterans, although the magnitude of the impact varies substantially across taxa. This distinct vegetation influences multiple components of the niche structure, such as feeding resources, breeding/oviposition sites (Tews et al., 2004) and shelter (Godinho et al., 2011) that greatly influence the mechanisms controlling local biodiversity (Lengyel et al., 2016; Stein et al., 2014). Moreover, the diverse microclimates created by a dense shrub layer (Cuesta et al., 2010) may be suitable for species that are unable to live in the surrounding shrub-free wood-pasture matrix.

In Coleoptera, the assemblages of the shrubby patches and matrix were greatly distinct (Table 2). Beetles are trophically diverse, feeding not only on living plants but also on fungi, plant debris, invertebrates, etc. Thus, patches offer them distinct niches at several trophic levels, influenced not only by floristic composition but also by factors like microclimate, leaf litter and prey availability. Moreover, the closed shrub layer in patches may create microclimates that allow the presence of beetles with distinct thermal tolerances (Taboada et al., 2006). The shadowing by these same shrubs also reduces the density of the herb layer, which for the many species of highly mobile ground beetles represents a dramatic change of habitat (Aviron et al., 2005). Differences in vegetation and microclimate are likely to result in a distinct leaf litter, also reported to influence beetle assemblages (Koivula et al., 1999; Doblas-Miranda et al., 2009). Some invertebrate species were also observed to be specific to ungrazed patches which had higher herbaceous biomass and litter than grazed patches (Bugalho et al., 2011b).

The unique physiological characteristics of lichens make them highly sensitive to a variety of environmental factors (Pinho et al., 2009; 2011) that are distinct between the patches and the matrix. In the matrix we only observed epiphyte and saxicolous lichens; in the patches these appeared in a greater diversity and, in addition, we had species that grow on mosses. Much of the distinctiveness in lichen

communities between the patches and with the matrix is presumably due to differences in microclimate (Ellis and Coppins, 2010; Matos et al., 2015) and light penetration, and to a greater variety of plant substrates (Marini et al., 2011; Giordani et al., 2013). Rocky outcrops may also play a role in driving the observed differences in lichen communities by providing a distinct substrate. As expected, saxicolous species were generally more abundant in the patches that had rocks on the ground. In the lichen ordination of Freixo do Meio study area (Fig. 3A), we observed that P5, P8 and P9 grouped closer to the matrix sites. These patches either do not include rocks or they have fewer rocks (Table S1). This may indicate that lichen composition in more open patches, where grazing is less excluded, might become similar to the matrix sites over time. In addition, differences in grazing pressure inducing changes in soil nutrient composition, soil moisture (Rolo et al., 2012; Rolo et al., 2013) and in humidity (Aragón et al., 2010) may contribute to differentiation in the lichen composition between the patches and matrix.

In conclusion, patches had distinct species assemblages for all the studied taxa, although the degree of distinctiveness varied among taxa. The presence of large exposed rocks on most patches may help explain some of the differences, because they add a distinct substrate, but even patches without rocks are very distinct from the matrix (Fig. 2). It is thus evident that the small size of the patches does not prevent their species assemblages from becoming clearly distinct from those of the matrix and thus their presence introduces a substantial ecological diversification in areas dominated by wood-pastures. This may result in an overall increase in landscape biodiversity, as discussed in the next section.

4.2. Small shrubby patches substantially enhance species richness of wood-pasture landscapes

Our data show that the species assemblages of the small shrubby patches are markedly distinct from those of the matrix across a very diverse set of taxa. However, to evaluate the usefulness of using such small patches for improving the biodiversity wealth of wood-pasture landscapes it is important to

determine the magnitude of the gains obtained by adding the patches. Our results show that patches substantially increase species richness in both study areas (Fig. 4). In our study this increase varied between 27% and 42%, depending on the taxonomic group, which represents a major gain taking into consideration the very small area covered by patches in the studied wood-pastures. However, it is important to note that the increases in richness that we estimated in this study are only approximate, and that such estimates may be influenced by sampling strategies. The lack of a significant influence of rock cover on plant and beetle richness (Table 3) indicates that rock cover is not confounding the effect of the shrub cover. Rock cover only has a positive impact on lichen species richness (Table 3). This result supports that the presence of rocks may facilitate the colonization of different lichen species, namely saxicolous species, in shrubby patches.

The increase in overall landscape biodiversity is a direct consequence of the substantial habitat diversification provided by the patches, and other studies have also found similar gains with the incorporation of various types of landscape elements in production land (Benton et al., 2003; Moreno et al., 2016; Simonson et al., 2018). In the case of the previously mentioned Woodland Key Habitats (WKH) approach, small protected patches have also been found to enrich the biodiversity of production boreal forest in northern Europe (Timonen et al., 2011). It is, however, important to note that the patches used in the WKH often differ from the habitat matrix in terms of soil or hydrological conditions and although small, tend to be larger than those involved in our study. The most common and better studied type of landscape element diversifying production land are hedgerows of woody vegetation, present in many agricultural landscapes. In farmland they are known to have a great positive impact on many components of biodiversity (Graham et al., 2018). However, the impact of hedgerows is presumably greater than that of the small patches that we studied or those used in WKH, because they are often long and interconnected structures, and thus greatly facilitate the dispersal of taxa.

It is worth mentioning that the positive impact of the shrubby patches is likely to extend well

into the wood-pasture matrix. Our study was not designed to detect this effect, but studies done on small galleries of riparian vegetation embedded in a matrix of Mediterranean wood-pastures found that they increase species richness up to more than 100 m into the matrix, in groups as diverse as birds and beetles (Silva et al., 2008; Leal et al., 2011).

The studied vegetation patches are in general too small to hold even just one full breeding territory of vertebrates like birds or mammals, but this does not mean that they do not have a positive impact on the species richness of their species assemblages and on population connectivity. For example, shrubby patches make available distinct nesting and feeding resources, such as berries, which are important for many bird species present in wood-pasture landscapes. Likewise, there are species of other groups of vertebrates that forage mostly in the matrix but use the patches as refugia. Although we did not study this phenomenon, we found abundant evidence of species like rabbits, carnivores and wild boar roosting in the patches, so it is possible that patches play a role similar to wooded hedgerows, which are used as refuges by a great variety of vertebrates (Lecq et al., 2017).

5. Implications for conservation

Thanks to their great biodiversity value and threatened status, several types of wood-pasture have been classified as High Nature Value Farmland or are protected under the EU Habitats Directive. This is generating regulatory and financial opportunities to maintain and further enhance their natural value. As these instruments become available, it is critical that managers and conservationists have strategies to improve management, without compromising the sustainable exploitation of the system. The development of these solutions is currently an important area of research (Leal et al., 2018) and we hope that the strategy here proposed of allowing the establishment and maintenance of shrubby patches within the matrix becomes part of the set of management tools available to improve wood-pastures and

is included in policy directives and certification schemes.

The virtual elimination of the shrub layer, usually present in the original vegetation of the areas now covered with wood-pasture (Bergmeier and Roellig, 2014), is bound to represent a major constraint for the richness of its species assemblages. However, our results show that allowing spontaneous shrubby vegetation to recover, even in small patches (median value: 1009 m^2), has a very substantial positive impact on the biodiversity of wood-pastures. This indicates that the protection of even very small shrubby patches is a potentially efficient strategy to increase the biodiversity value of wood-pastures, although it would be desirable to further study this, particularly in different types of wood-pasture.

It is very important to note that a strategy based on the preservation of very small patches scattered in a matrix of semi-natural wood-pasture is not a replacement for the protection of large contiguous tracks of the original natural habitat. Species mostly dependent of habitat with well-developed undergrowth and having large home ranges, are unlikely to be able to take advantage of the small patches. The species that are most likely to benefit from the addition of patches are either those that can maintain viable populations in very small areas, such as some plants and invertebrates, or those that are mostly dependent on foraging resources in the matrix but use the patches for cover. An example is the European rabbit *Oryctolagus cuniculus*, which prospers in the interface between shrubland and grassland (Lombardi et al., 2003) and is in turn a critical resource for many highly threatened vertebrates, such as the Iberian lynx (*Lynx pardinus)* and the Iberian Imperial Eagle (*Aquila adalberti)*, both known to use Mediterranean wood-pastures if prey are sufficiently abundant.

The main advantages of the proposed strategy to increase the biological value of wood-pastures are its low cost and ease of implementation. In fact, the income lost due to a decrease in grazing surface is minimal because of the small area occupied by patches. It is often possible to establish them in places where maintaining open pasture is difficult, as in the case of the rocky ground that protects the

patches in our study area. In addition, small fenced enclosures can be also used to stimulate shrub regeneration and growth in non-rocky or very open rocky areas, which are presently exposed to grazing. In many situations the regeneration of the vegetation in the patches is spontaneous (Príncipe et al., 2014), and in our study areas the resulting patches were dominated by species that were presumably part of the original Mediterranean woodland (Basnou et al., 2016). However, planting native shrubs may help accelerating regeneration and promote the most desirable species, such as those that produce berries, a resource that seems to be limiting at least in Mediterranean wood-pastures (Tellería, 2001; McCarty et al., 2002).

Further research is needed to understand to what extent the biodiversity enhancement strategy that we evaluated here is applicable to the distinct types of woody-pasture existing in Europe and other temperate regions. Additionally, in the case of establishment of the patches, there may be potential issues requiring further consideration such as founder effects, inbreeding risk and vulnerability to local extinction (Rey Benayas et al. 2008). However, our study indicates that implementing this strategy can result in substantial conservation gains, at low cost and without compromising the economic value of a type of landscape that is an important part of the natural and cultural heritage of Europe.

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Table S1: Characteristics of sampled ungrazed patches in Freixo do Meio and Barrocal dos Ricos; patch area, height of woody vegetation (excluding trees), and proportion of ground covered by exposed rocks (on a scale of 0 to 5).

Sites	Patches	Patch size (m^2)	Height of the understory (m)	Index of rock cover
Freixo do Meio	**P1**	927	3	3
	P2	607	5	2
	P3	579	6	1
	P4	1009	5	1
	P5	3000	3	0
	P6	2500	1	0
	P7	252	5	0
	P8	402	5	0
	P9	1195	5	1
Barrocal dos Ricos	**P10**	1520	3	1
	P11	889	3	1
	P12	1044	3	1
	P13	2015	2	2

Table S2: Presence-absence data of plants, lichens and coleopterans.

Site	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix
Area	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	BR	BR	BR	BR	BR	BR	BR	BR
Quercus rotundifolia	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	1	1	1	1	0	0	0	0
Quercus suber	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Olea europaea	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
Quercus coccifera coccifera	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smilax aspera	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryonia dioica	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Rubia peregrina	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus ulmifolius	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnus alaternus	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Pistacia lentiscus	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnus lycioides oleoides	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asparagus aphyllus	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ruscus aculeatus	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cistus salviifolius	0	0	0	1	0	1	1	1	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0
Daphne gnidium	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Calamintha nepeta nepeta	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Arum italicum italicum	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Urginea maritima	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Asphodelus ramosus	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Muscari comosum	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0
Polypodium cambricum cambricum	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Andryala integrifolia	0	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0
Crepis vesicaria taraxacifolia	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0
Cynara humilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Leontodon taraxacoides	1	0	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1
Senecio jacobaea	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Echium plantagineum	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0	0	0	1	1	1	1
Silene vulgaris vulgaris	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
Umbilicus rupestris	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Plantago coronopus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0
Plantago lagopus	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	0	0	0	1	0	1	0
Dactylis glomerata	0	1	1	1	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0	0
Digitalis purpurea	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Lotus corniculatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Trifolium repens	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Cynodon dactylon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Holcus lanatus	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Rumex acetosella angiocarpus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Rumex pulcher woodsii	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	0	0	0
Torilis arvensis	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Carduus tenuiflorus	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0
Crepis capillaris	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	0
Hypochaeris glabra	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0
Sonchus oleraceus	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Urospermum picroides	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Sisymbrium officinale	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Teesdalia nudicaulis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cerastium glomeratum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0
Illecebrum verticillatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Polycarpon tetraphyllum tetraphyllum	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0
Silene gallica	0	0	0	1	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	0	1	0	1
Tuberaria guttata	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0
Medicago polymorpha	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	0	1	1	1	0
Ornithopus compressus	0	0	0	1	0	0	1	0	1	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0
Trifolium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Trifolium arvense	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0
Trifolium glomeratum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Geranium molle	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	0	0
Geranium robertianum	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
Juncus bufonius	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0
Juncus capitatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Stachys arvensis	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0
Avena barbata	0	0	0	1	1	1	0	1	0	1	1	1	1	1	1	1	0	0	0	0	0	1	0	1
Bromus diandrus	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	1	1	1	0	0	0	0
Bromus hordeaceus	1	0	0	1	0	0	1	0	0	1	0	1	1	1	1	1	0	0	0	0	1	1	0	0
Bromus madritensis	0	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cynosurus echinatus	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Holcus annus	0	0	0	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1
Hordeum murinum	0	0	0	1	1	0	0	1	0	1	0	1	1	0	1	1	0	0	0	1	0	0	0	0
Vulpia myuros	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	1	1	1
Rumex bucephalophorus	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0
Anagallis arvensis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0
Galium aparine	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Parietaria mauritanica	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Urtica membranacea	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0

Site	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix
Area	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	BR	BR	BR	BR	BR	BR	BR	BR
Agonimia opuntiella	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	1
Aspicilia intermutans	1	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1	1	0	1	0
Bacidia iberica	0	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Bacidia polychroa	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Candelariella vitellina	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysothrix candelaris	1	1	1	1	1	1	0	1	0	0	1	0	1	1	1	0	0	1	1	1	1	0	0	1
Cladonia cf monomorpha	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladonia rangiformis	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collema furfuraceum	1	0	1	1	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0	1	1	1	1	1
Collema ryssoleum	0	0	0	1	1	1	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Dendrographa decolorans	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	1	1	1	0	0
Diploschistes scruposus	1	0	1	1	0	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0
Evernia prunastri	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1
Flavoparmelia caperata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hyperphyscia adglutinata	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lasallia pustulata	1	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Lecanora albella	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Lecanora campestris	1	1	1	1	0	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Lecanora chlarotera	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0
Lecanora hybocarpa	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Lecidella elaeochroma	1	0	1	1	1	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0
Melanelixia gabratula	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Melanelixia subaurifera	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Nephroma tangeriense	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Normandina pulchella	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ochrolechia parella	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0
Parmelia saxatilis	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0
Parmelia sulcata	0	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1	1	0	0	1
Parmelina tiliacea	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	1	1	0	1	1	1	0	0
Parmotrema hypoleucinum	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Parmotrema perlatum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pertusaria albescens	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1
Pertusaria amara	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pertusaria aspergilla	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pertusaria coccodes	0	1	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	0	0	0
Pertusaria flavida	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0
Pertusaria heterochroa	1	1	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0
Pertusaria pertusa	1	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	0	0	1	1	0	0	0	0
Phaeophyscia cernohorsky	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0
Phaeophyscia orbicularis	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Phlyctis agelaea	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Phlyctis argena	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Physcia adscendens	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Physconia perisidiosa	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Porina aenea	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1	0
Punctelia subrudecta	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyrrhospora quernea	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Ramalina canariensis	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
Ramalina farinacea	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ramalina fastigiata	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1
Ramalina geniculata	1	1	1	1	1	1	1	0	1	0	1	1	1	0	1	0	1	1	1	1	0	0	0	0
Rhizocarpon geographicum	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Teloschistes chrysophthalmus	1	1	0	1	0	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
Usnea rubicunda	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Waynea stoechadiana	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
Xanthoparmelia pulla	1	1	1	1	1	1	0	0	0	0	1	1	0	0	1	0	1	1	1	1	1	0	1	0
Xanthoparmelia tinctina	1	1	1	1	0	1	1	0	1	0	1	1	0	0	1	0	1	1	0	1	1	0	1	0
Xanthoria parietina	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0
Cladonia aff pyxidata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Collema sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Opegrapha sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Physcia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Physcia stellaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Usnea hirta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Xanthoparmelia conspersa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0

Site	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix
Area	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	BR	BR	BR	BR	BR	BR	BR	BR
Anobium punctatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Ptinus fur	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Ptinus sp.	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Omonadus floralis	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Malvapion malvae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Bruchidius jocosus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Bruchus loti	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bembidion (Phyla) tethys	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calathus (Neocalathus) granatensis	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Calodromius putzeysi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carabus (Macrothorax) rugosus celtibericus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Carabus (Mesocarabus) lusitanicus latus	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Laemostenus terricola	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pterostichus (Steropus) ebenus	0	0	0	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1
Platyderus portalegrae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trechus obtusus	0	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haltica sp.	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phylotreta sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cryptorhynchus lapathi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Graptus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Limobius borealis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Sitona sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0
Dicronychus cinereus	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Dicronychus equiseti	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lycoperdina bovistae	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Teretrius (Neotepretius) parasita	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Catops fuscus	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lampyris iberica	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leiodes sp.	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dorcus parallelipipedus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Meloe proscarabaeus proscarabaeus	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Serica brunea	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1
Attalus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Monotropus lusitanica	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Chasmatopterus hirtulus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paleostigus palpalis	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oryzaephylus surinamensis	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Ctenomastax kiesenweteri	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Geostiba sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxyporus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Quedius sp.	0	1	1	1	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0
Ocypus olens olens	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Tentyria platyceps	1	0	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	0	1	1	0	1
Akis granulifera	1	1	0	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Akis lusitanica	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Blaps lusitanica	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Trox perlatus hispanicus	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Bembidion (Neja) ambiguum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Calathus (Calathus) hispanicus dejeani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Scymnus (Pullus) suturalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Enicopus (Enicopus) scutellaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Attagenus trifasciatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Attagenus unicolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Carcinops (Carcinops) pumilio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Alphasida marseuli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Sepidium bidentatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0

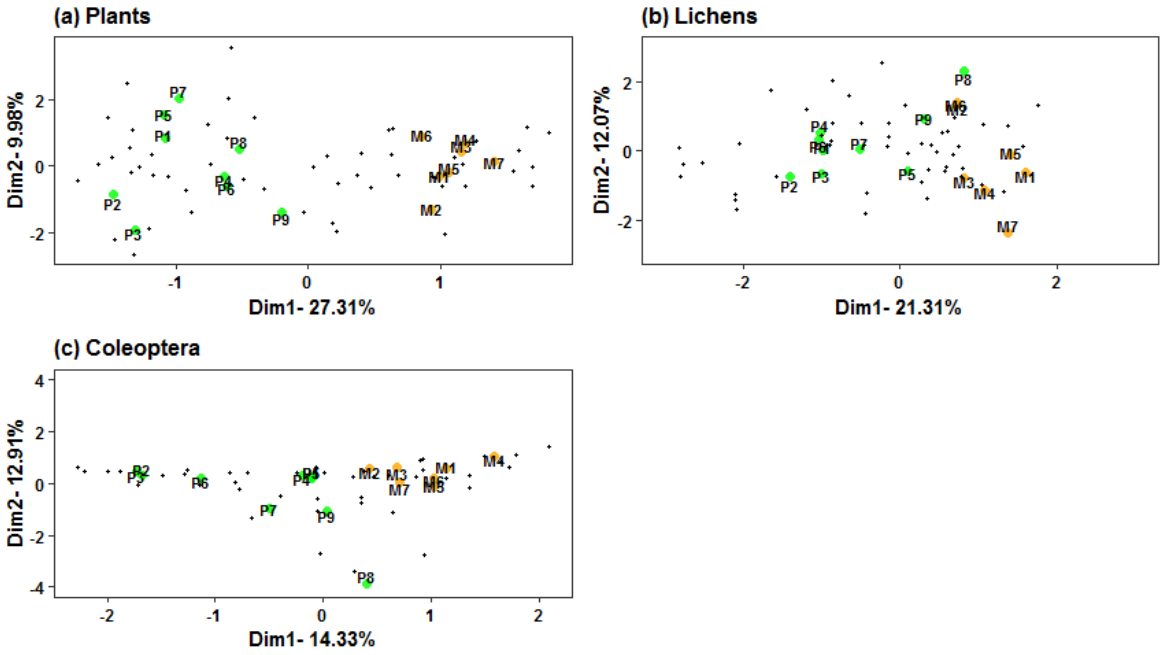

Figure S1. Correspondence analysis (CA) results of the sampled sites in matrix and ungrazed patches in Freixo do Meio, using each taxon separately.

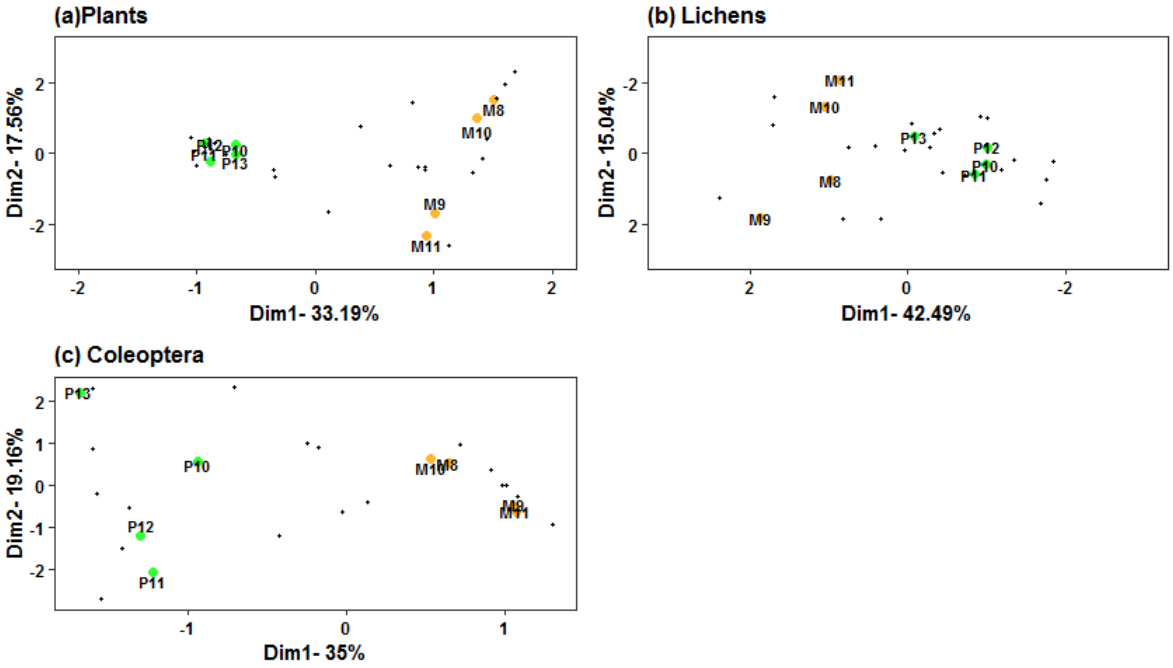

Figure S2. Correspondence analysis (CA) ordination of the sampled sites in matrix and ungrazed patches in Barrocal dos Ricos, using each taxon separately.

CHAPTER 3

The contribution of small shrubby patches to the functional diversity of wood-pastures

Oksuz, D.P., Aguiar, C.A., Tápia, S., Llop, E., Lopes, P., Serrano, A.R.M, Leal A.I., Branquinho, C., Correia, O., Rainho, A., Correia R.A., Palmeirim, J.M. **The contribution of small shrubby patches to the functional diversity of wood-pastures.** Submitted to Acta Oecologica (September 22, 2019).

Abstract

Wood-pastures are grazed landscapes resulting from a long-term use of natural woodlands by humans. These social-ecological systems, covering vast areas of Europe and other temperate regions, have both high biodiversity and economic values, so many are classified as High Nature Value Farmlands. However, in some regions a loss of spatial heterogeneity threatens this natural value. We investigated the potential contribution of tiny shrubby patches to increase spatial heterogeneity and functional diversity in wood-pasture landscapes. Specifically, we compared functional composition (Community Weighted Means) and functional diversity (Functional Dispersion and Functional Evenness) of assemblages of plants, beetles and lichens in those patches (252 to 3000 m^2) and in the wood-pasture matrix. We found that shrubby patches and matrix harbour species assemblages with very distinct functional compositions in all studied taxonomic groups. Evergreen, woody, broad-leafed, fleshy-fruited and zoochory-dispersed, are plant traits better represented in the patches. In beetles, the main differences were a greater prevalence of small-sized and fungivore species in the patches, which also harboured lichen assemblages with a greater prevalence of fruticose, foliose-broad, hygrophytic and oligotrophic traits. Moreover, the two indexes used to quantify functional diversity (Functional Dispersion and Functional Evenness) show that, overall, diversity is greater in patches than in the matrix; in patches Functional Dispersion is statistically higher for plants, and Evenness is statistically higher for beetles and lichen. These differences are all consistent with the very distinct ecological conditions in the matrix and patches. The greater overall functional diversity of shrubby patches, and the major differences in functional composition between patches and matrix, observed in all taxa, indicate that patches greatly enhance spatial heterogeneity and functional diversity of species assemblages in wood-pasture landscapes. Consequently, preserving and promoting tiny shrubby patches is a potentially valuable low-cost management tool to increase biodiversity and improve

ecosystem functioning in wood-pasture landscapes.

Keywords: functional diversity; habitat management; montado/dehesa; multi-taxa; native vegetation; silvopasture

1. Introduction

Wood-pastures are savanna like systems, common across Europe, that have been shaped by a long-term history of animal grazing and the interaction between various land-use regimes and natural factors (Hartel and Plieninger, 2014). They often have a high economic value resulting from the combined exploitation of livestock grazing and various timber (such as firewood, cork, etc.) and non-timber forest products (Plieninger et al., 2015; Moreno et al., 2017). Despite their anthropogenic character, wood-pastures often retain many features of their original natural vegetation and support a rich biodiversity (Bugalho et al., 2011; Bergmeier and Roellig, 2014). As a consequence, many wood-pastures in Europe are considered High Nature Value Farmlands (HNVF), agricultural landscapes holding a high biodiversity value, often as a result of a high spatial habitat diversity (Andersen et al., 2003; Pinto-Correia and Ribeiro, 2012). For example, it has been shown that in a context of wood-pasture the presence of landscape elements such as lines of riparian vegetation or small orchards can increase landscape level species diversity in arthropods (Taboada et al., 2006; Silva et al., 2011), birds (Leal et al., 2011) and mammals (Diaz et al., 1997; Rosalino et al., 2009).

Despite their widely recognized economic and biodiversity value, wood-pastures are reportedly declining due to land-use changes driven mostly by intensification or land abandonment (Bugalho et al., 2009; Godinho et al., 2014). In some regions, traditional land-uses have been greatly simplified, or even abandoned, due to changes in the market value of products and rural socio-economic conditions, resulting in human migration to urban areas (Plieninger et al., 2015). In more productive regions,

changes in livestock type and increasing animal densities have been observed, generally in response to changing market incentives, resulting in higher grazing pressure (Pinto-Correia and Godinho, 2013). Livestock grazing is an important aspect of wood-pasture dynamics as it usually contributes to maintain the characteristic vegetation structure and spatial heterogeneity (Moreno and Pulido, 2009). However, most intensively managed wood pastures end up being dominated by just two vegetation layers, an herb layer and a tree layer of variable density, because the regeneration of shrubs is repressed mechanically or by intensive grazing (Sales-Baptista et al., 2015; Listopad et al., 2018). The near or total absence of a shrub layer results in a simplified habitat structure and reduced spatial heterogeneity, with potential negative consequences for the natural value of wood-pastures.

Nevertheless, even intensively managed wood-pastures are occasionally dotted with small patches that are naturally excluded from grazing and mechanical clearing (e.g. rocky outcrops). The vegetation in these patches consists mostly of native trees, shrubs and herbs that are often representative of local forest communities before human intervention (Bergmeier et al., 2010). They contrast with the wood-pasture matrix of open and regularly grazed pastures (henceforth referred to as "matrix") in terms of micro-climatic conditions, soil nutrients, shelter availability and food resources and may thus be an important contribution to the spatial heterogeneity in wood-pastures (García-Tejero and Taboada, 2016). However, it remains to be assessed if this ecological diversification results in an increase of ecosystem function by adding to the assemblage species belonging to functional groups that are distinct from those present in the wood-pasture matrix. If the species added by the presence of patches are functionally redundant with those in the matrix, there will be no overall change in functional diversity despite the increase in species richness. Understanding the functional contribution of small shrubby patches can contribute towards the development of biodiversity-friendly management solutions that address the adverse effects of land-use intensification and landscape homogenization,

without restricting the social and economic benefits of wood-pastures. Because functional diversity is an important driver of ecosystem services and processes (de Bello et al., 2010; Gagic et al., 2015), maintaining or expanding such patches could prove effective to promote spatially-heterogeneous, species-rich and functionally diverse habitats. However, to our knowledge, the contribution of shrubby patches to the functional diversity of wood-pastures has not been studied, so the information available across multiple biological groups and at appropriate spatial scales is too scarce to support management decisions.

In this study, we address this knowledge-gap using as a case study the Iberian wood-pasture system generally known as *montados* or *dehesas*, which covers vast areas throughout the western Mediterranean (Pinto-Correia et al., 2011). Their savannah-like structure has a tree layer usually dominated by cork oaks (*Q. suber*) and/or holm oaks (*Q. rotundifolia*). They are typically exploited for livestock grazing and cork or acorn production and, due to their rich biodiversity, are classified as High Nature Value Farmland. Like in most other wood-pasture systems, the intensively managed and grazed areas usually lack a well-developed shrub layer. We aimed to assess the contribution of very small shrubby patches to wood-pasture functional diversity by comparing shrubby patches and the wood-pasture matrix using indices of functional composition (Community Weighted Means) and diversity (Functional Evenness and Functional Dispersion) across multiple taxa. Specifically, we address the following questions: 1) Are there trait-level differences in functional composition between shrubby patches and the matrix? And 2) do shrubby patches contribute to the functional diversity of landscapes dominated by wood-pastures? We explore these questions using three distinct taxonomic groups - plants, beetles and lichens. These groups were chosen as they potentially respond to important ecological factors such as direct grazing pressure (plants), vegetation structure (beetles), and micro-climatic conditions and nutrient availability (lichens).

2. Materials and Methods

2.1 Study Area

Our study was done at two wood-pasture areas representative of the typical *montado* system, located in southern Portugal. The region has a Mediterranean climate, with hot and dry summers (Agencia Estatal de Meteorología, 2011). Small shrubby patches are common in the study area, often associated with rocky outcrops where it is difficult to clear shrubs; as the shrub layer in the patches develops livestock tend to stop grazing in them. They usually host an ensemble of cork/holm oaks (*Q. suber/Q. rotundifolia*), wild olive trees (*Olea europaea* var. *sylvestris*) and fruiting evergreen shrub species such as evergreen buckthorn (*Rhamnus alaternus*) and elm leaf blackberry (*Rubus ulmifolius*). Shrubby patches are usually small but highly variable in terms of size, shrub density, woody plant richness and composition, and may constitute a substantial source of habitat heterogeneity in wood-pasture landscapes.

Sampling was conducted during 2012-2013 in a total of twenty-four plots of which 13 in shrubby patches (henceforth *patches*, N = 13) and 11 in the nearby wood-pasture matrix (henceforth *matrix*, N = 11), at the two wood-pasture areas, Herdade do Freixo do Meio (FM) (38º 42'N, 8 º 19.1'W) and Barrocal dos Ricos (BR) (38º 46'N, 8 º 15'W) (Fig 1). Mean annual rainfall in the region is around 662 mm and the mean annual temperature around 16.1 °C (Hijmans et al., 2005). The matrix of *montados* in the study area is mostly grazed by sheep and cattle and used to raise pigs that feed mainly on acorns. The wood-pasture areas (FM and BR) are located about 10 km from each other and in both areas all sampled plots are located within a radius of less than 1 km. The sampled patches varied in size, from 252 m^2 to 3000 m^2. The matrix plots were selected randomly within the same block of the sampled shrubby patches and they were at least 100 m distanced from each other and at least 140 m away from the patches. The tree cover was around 30 trees/ha in the matrix. The number of matrix

plots and patches is not the same because we had to exclude the interfered pitfall traps by the pigs and wild boars from the sampling.

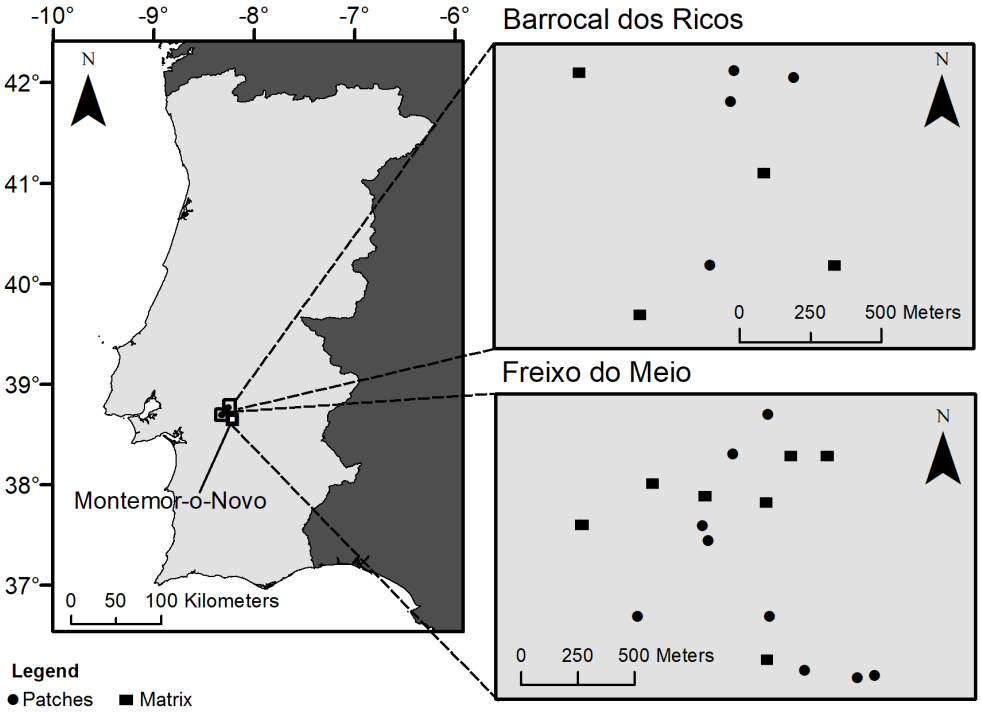

Fig. 1. Map of the study areas located in Montemor-o-Novo county, Portugal. Circles represent patches and filled squares represent matrix plots in Freixo do Meio and Barrocal dos Ricos.

2.2 Plant sampling

We sampled shrubs, grasses and forbs at both the patches and matrix plots using the Braun-Blanquet method with a 100 m^2 (10x10 m) quadrat (Kent and Coker, 1996) between May and July 2013. The cover of each plant species in the quadrat was visually estimated by the same observer. In each native patch a quadrat was placed just clearly inside the patch, with one of the sides along the edge of the patch. The quadrats were placed along the edges of the patches since the dense shrub layer of some patches did not allow to sample the deeper inside of these plots. In the matrix all quadrats

included areas with and without canopy cover. Plant species present in each quadrat were identified in the field or in the laboratory, and their abundance was recorded using the Braun-Blanquet cover-abundance scale scored from 1 to 5 (Kent and Coker, 1996). For statistical analysis these scores were converted to a percentage scale ranging from 2.5% to 87.5% (1=2.5%, 2=15%, 3=37.5%, 4=62.5%, 5=87.5%) (Table S1).

To characterize the functional composition of the matrix and shrubby patches we selected six functional traits defining distinct vegetation characteristics that potentially reflect the differences in grazing pressure between the patches and matrix: woodiness, growth form, leaf shape, leaf phenology, fruit type and dispersal strategy traits (Table 1; Tables S2 and S3). Trait data for most species was extracted from the BROT database (Paula et al., 2009; Tavşanoğlu and Pausas, 2018). For species not in this database, we used the TRY (Fitter and Peat, 1994; Castro-Díez et al., 1998; Kühn et al., 2004; Kattge et al., 2011) and LEDA (Kleyer et al., 2008) databases and published resources (Herrera, 1995; Manzano and Malo, 2006; Lengyel et al., 2009; Guzmán and Vargas, 2009; Groom and Lamont, 2015; Linder et al., 2017). A description of each plant trait and their related trait syndromes is presented in Table 1.

Table 1

Comparison of community weighted mean (CWM) values using Wilcoxon rank sum test between the matrix and patches for the traits of plants, beetles and lichens. The values of *p* and W resulted from Wilcoxon rank sum test ($p \leq 0.05$).

Taxa	Traits	Categories /Unit	*p*	W
PLANTS	**Woodiness**	Woody	**<0.001**	0
		Non-woody	**<0.001**	143
	Growth form	Tree	**<0.001**	3
		Shrub	**<0.001**	0
		Herb	**≤0.005**	138
		Graminoid	**<0.001**	141
	Leaf shape	Broad	**<0.001**	3
		Linear	**<0.001**	140
	Leaf phenology	Evergreen	**<0.001**	0
		Deciduous	**0.01**	116
	Fruit type	Fleshy fruit	**<0.001**	0
		Dry fruit	0.45	79
	Dispersal strategy	Zoochory	**<0.001**	0
		Autochory	0.69	79
		Allochory	0.7	141
BEETLES	**Body size**	mm	**0.02**	111
	Feeding guild	Predator	0.55	77
		Herbivore	0.36	88
		Saprovore	0.94	77
		Fungivore	**0.03**	28
	Dispersal strategy	Brachypterous	0.22	64
		Dimorphic	0.24	55
		Macropterous	0.07	96
LICHENS	**Growth form**	Crustose	0.07	37
		Foliose narrow-lobed	**≤0.005**	128
		Foliose broad-lobed	**0.02**	32
		Fruticose	**0.01**	17
		Squamulose	0.7	72
	Photobiont type	Chloroccocoid	0.30	42
		Trentepohlia	0.40	94
		Cyanolichen	0.46	76
	Reproduction strategy	Asexual sorediate	0.78	66
		Asexual isidiate	0.82	79
		Sexual	0.88	57

		Categories /Unit	*p*	W
	Humidity preference	Hygrophytic	**0.05**	25
		Mesophytic	0.95	35
		Xerophytic	**0.01**	110
	Eutrophication tolerance	Oligotrophic	**≤ 0.005**	4
		Mesotrophic	0.79	88
		Nitrophytic	**≤0.005**	120

2.3 Beetle sampling

Beetles were sampled in each individual plot using sets of three pitfall traps buried in the soil, with the top level with the surface of the ground. They were made from polystyrene cups with a 95 mm diameter and were filled with water, soap and salt to a depth of 3 cm. Traps were active for 5 weeks from 20th May to 25th June in 2013, but the captured arthropods were removed weekly. Captures in the same patch or matrix site were pooled before analyses. All Coleoptera species were identified to species level and the number of captures of each taxon was recorded (Table S1).

We used body length, feeding guild and dispersal strategy traits to characterize the beetle species assemblages (Table 1; Tables S2 and S3). Body length was measured in the laboratory from the tip of the head to the tip of the abdomen for 5 individuals of each species and averaged for the species. Feeding guilds were collected from available databases (Homburg et al., 2014) and published resources (Harde and Severa, 1984; Baraud, 1992; Viñolas and Cartagena, 2005). The hind wing morphology of each species was recorded from sampled individuals to define the dispersal ability trait (Aukema, 1986; Desender, 1989; Homburg et al., 2014).

2.4 Lichen sampling

Lichen sampling was performed by the same observer using the European standard protocol

(Asta et al., 2002) between December 2013 and January 2014. All cork oaks (*Q. suber*) and holm oaks (*Q. rotundifolia*) with a diameter at breast height (dbh) greater than 15 cm (always fewer than five) were selected for sampling in patches. In matrix, we sampled a fixed number of five trees per patch. A 10 x 50 cm frame divided into five 10x10cm grid-cells was vertically placed over each tree trunk at about 1 m above the ground. Each lichen species occurring inside each grid cell was identified to species level and recorded. This process was repeated in the four different orientations (N, S, E, W) and the number of quadrats where each species was identified was used to estimate species abundance (Table S1).

For each species recorded, we then collected information on five traits representing resource use characteristics (water and nutrient uptake) and dispersal ability of lichens from the ITALIC database (Nimis and Martellos, 2017). These traits included growth form, photobiont type, reproduction strategy, humidity preference and eutrophication tolerance. All lichen traits, and their associated groups used for the analysis are listed in Table 1 and Tables S2 and S3.

2.5 Data analysis

We tested differences in functional composition between the wood-pasture matrix and shrubby patches using the community weighted mean (CWM) index. This index represents the average trait value in a community, and it was estimated for each trait using species-trait and species-abundance matrices. In the case of continuous traits, the CWM is the weighted mean of that trait in the community, in which each species is weighted by its relative abundance. In categorical and binary traits CWM is the proportion of each category in the community (i.e. representing their relative abundance) (Lavorel et al., 2007).

Multi-trait functional dispersion (FDis) and functional evenness (FEve) indices were used to

characterize and compare the functional diversity of the three taxonomic groups in patches and matrix. Functional dispersion (FDis) measures the degree of dissimilarity in a community by calculating the weighted mean distance of each species to the weighted centroid of all species in multidimensional trait space of the community, with weights corresponding to species relative abundances. Functional evenness (FEve) index measure the evenness of species abundances distribution in the community trait space. These indices were selected because they can be calculated for any type of trait data (e.g. numerical, binomial, categorical) and are independent from species richness (Mason et al., 2005; Villéger et al., 2008). Before each index was calculated, we assessed the correlation between traits using Spearman correlations because highly correlated traits may bias measurements of functional diversity. There were no significant correlations ($p > 0.05$), so we calculated the multi-trait functional diversity indices using all traits compiled for each taxon, giving each trait an equal weight.

Community weighted mean (CWM), functional dispersion (FDis) and functional evenness (FEve) differences between the patches and the matrix were compared with Wilcoxon rank sum tests ($p \leq 0.05$) (Hollander and Wolfe, 1973). All indices were calculated using the 'dbFD' function in package 'FD' (Laliberté et al., 2014), Wilcoxon rank sum test was applied using "wilcox.test" function in "stats" package, and figures were produced using "ggplot2" (Wickham, 2009) in R v.3.4.3 computing environment (R Core Team, 2016).

We also tested whether the spatial distance between sampling sites had any effects on functional diversity and structure using a Mantel test (Mantel, 1967; Sokal, 1979), implemented with "ade4" package (Bougeard and Dray, 2018) also in R v.3.4.3, but no statistically significant ($p>0.05$) spatial effects were detected.

3. Results

3.1 Shrubby patches and the matrix host assemblages of plants, lichens and beetles with very distinct functional compositions

We identified a total of 73 species of plants, 57 of lichens and 43 of beetles. We detected highly significant differences in plant trait CWM values between patches and matrix for several of the trait syndromes tested (Fig 2 and Table 1). Plants with evergreen and woody growth forms, broad-leafed, with fleshy fruit and zoochory dispersal traits were much better represented in the patches than in the matrix. In contrast, linear-leaved plants and herbs were better represented in the matrix than in the patches (Table 1). There were no differences between matrix and patches in the relative abundance of plants with dry fruits, allochorous and autochorous dispersal (Table 1).

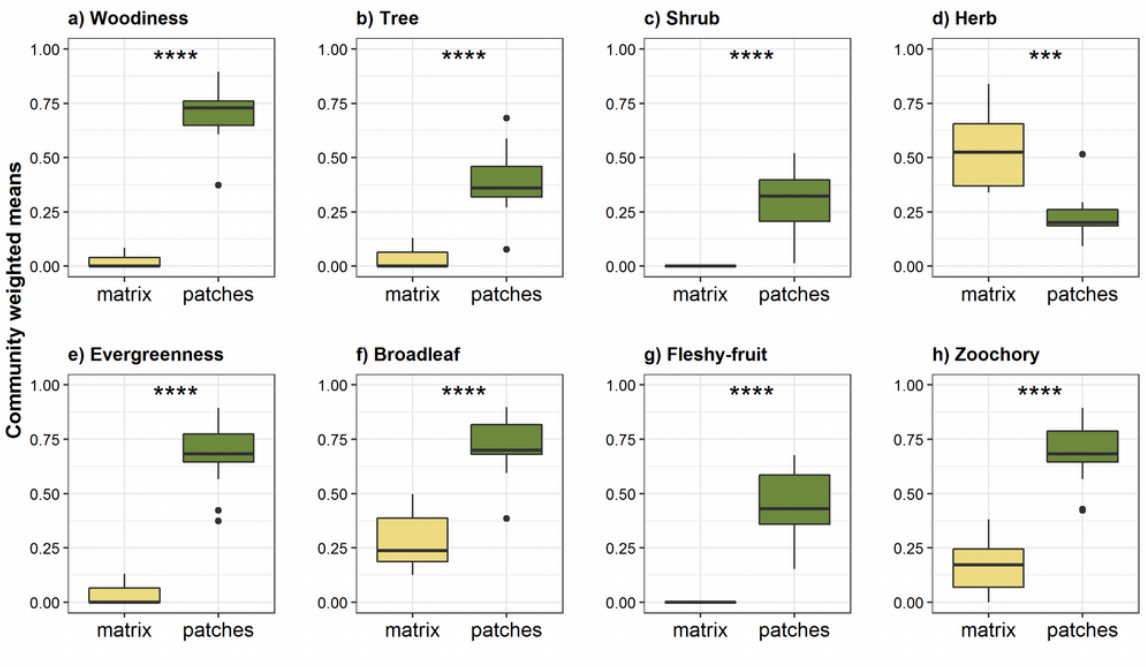

Fig. 2. Comparison of community weighted means (CWM) of plant traits in wood-pasture matrix and shrubby vegetation patches. Boxes show the median, lower and upper quartiles, whiskers represent extreme values and dots outliers. All differences are highly significant (**** $p < 0.001$, *** $p \leq 0.005$). See Table 1 for details on test statistics.

In beetles, CWM values of body size and fungivore feeding guild significantly differ between habitats, with small body-sized and fungivore species more prevalent in patches than in the matrix (Fig 3). We did not observe differences for saprovore, herbivore and predator feeding guilds (Table 1). Dispersal strategies did not differ between the patches and the matrix, but there is a nearly significant greater abundance of macropterous beetles in the matrix (Table 1).

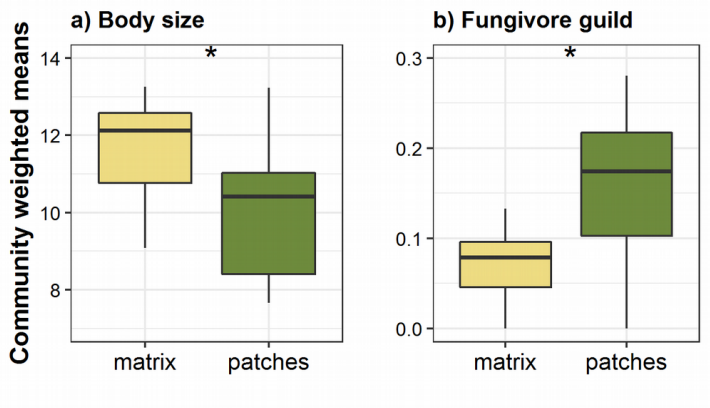

Fig. 3. Comparison of community weighted mean (CWM) for (a) body size and (b) fungivore beetle guilds. Smaller beetles and fungivore species were more prevalent in patches than in the matrix. Boxes identify the median, lower and upper quartiles, and whiskers show extreme values. Asterisks (*) indicate significant differences ($p \leq 0.05$). See Table 1 for details on test statistics.

In lichens, CWM values of fruticose and foliose-broad lobe growth forms are higher in patches, while foliose-narrow lobes species are higher in the matrix (Fig 4). The CWM for crustose or

squamulose growth lichens were not significantly different between habitats, although the difference was nearly significant in the former (Table 1). We did not observe any differences in lichen photobiont type and reproduction strategy traits (Table 1). Hygrophytic and oligotrophic lichen functional groups had higher CWM in the patches, and xerophytic and nitrophytic in the matrix (Fig 4). Mesophytic and mesotrophic lichens are similarly prevalent in patches and matrix (Table 1).

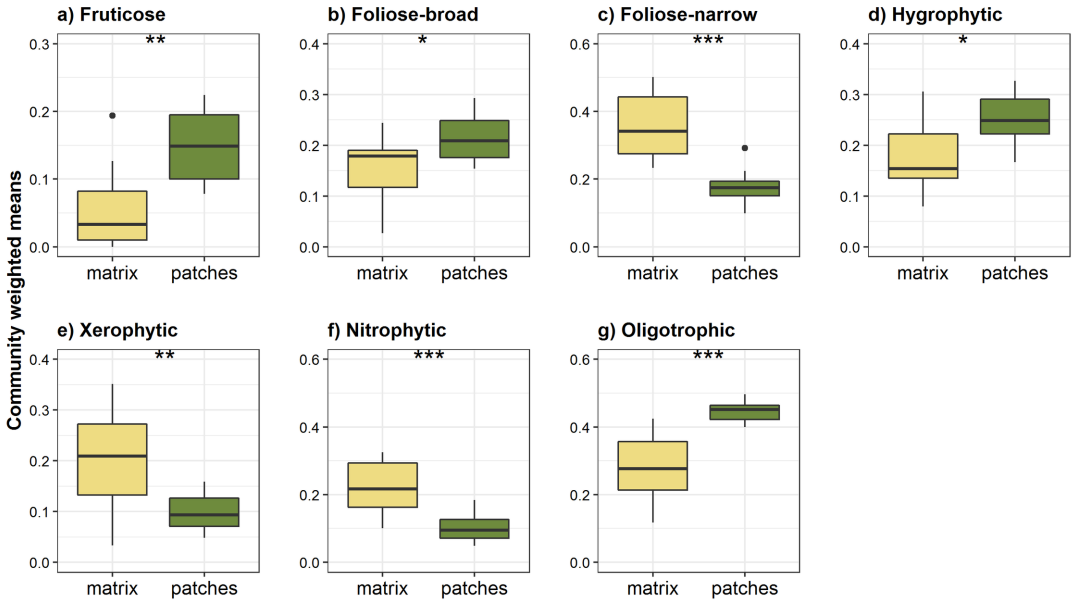

Fig. 4. Comparison of community weighted mean (CWM) in patches and matrix for lichen traits, Growth form (a), (b) (c); Humidity preference (d), (e) and Eutrophication tolerance (f), (g). Fruticose (a) and foliose-broad growth forms (b) as well as hygrophytic (d) and oligotrophic (g) lichens are better represented in patches than in the matrix. Boxes show the median, lower and upper quartiles, whiskers show extreme values and dots outliers. Asterisks indicate significant differences (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.005$, **** $p < 0.001$). See Table 1 for details on test statistics.

3.2 Functional dispersion and evenness in shrubby patches and matrix

Functional dispersion was significantly higher in patches than in the matrix for plants (W=5,

p=0.003), but there were no significant differences for beetles and lichens. Functional evenness (FEve) values are not different between the patches and the matrix for the plants. However, both beetles (W = 33, p-value = 0.03) and lichens (W = 29, p-value = 0.02) have significantly higher FEve value in the patches than in the matrix (Fig 5).

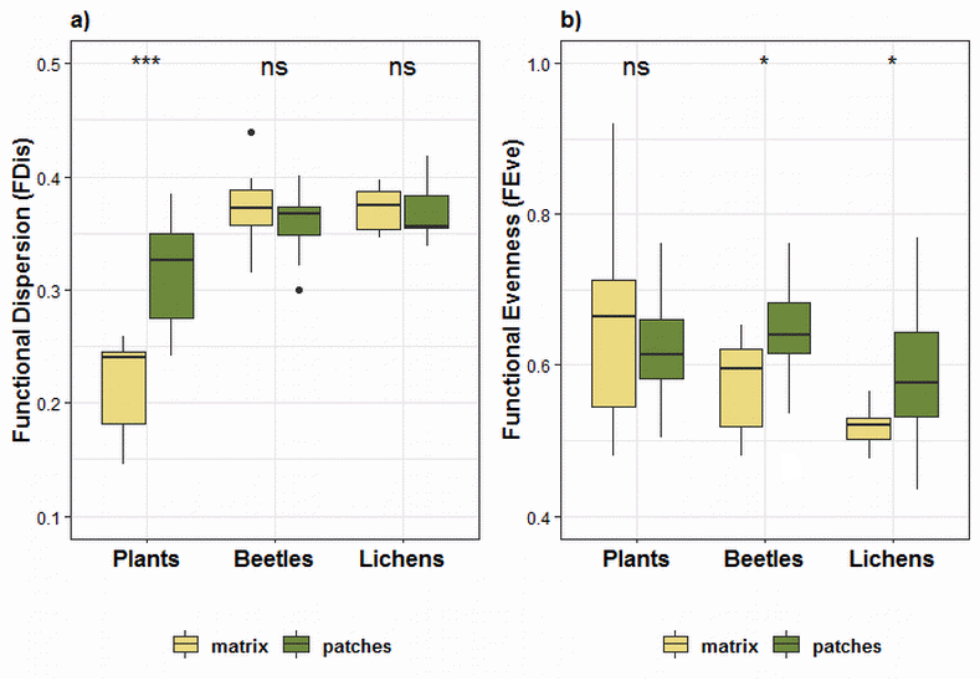

Fig. 5. Functional dispersion (a) and functional evenness (b) of plants, beetles and lichens in patches and matrix. Functional dispersion of plants is greater in patches than in the matrix, but differences for beetles and lichens are not significant. Functional evenness (FEve) is higher for beetles and lichens in patches than in the matrix, while it is not different for plants between the treatments. Boxes show the median, lower and upper quartiles, whiskers show lower and upper extreme values of FDis and FEve values and black dots are outliers. Asterisks indicate significant differences (* $p \leq 0.05$, *** $p \leq 0.005$) and ns indicates non-significant results ($p>0.05$).

4. Discussion

Our results show substantial trait-level differences between shrubby patches and the wood-

pasture matrix in the species assemblages of the three studied taxonomic groups. To begin with, shrubby patches have a higher diversity and relative abundance of woody plants, often with evergreen broad leaves and fleshy-fruits with zoochorous dispersal. In contrast, the open matrix is dominated mostly by linear-leaved and dry-fruited herbs (Fig. 2). Functional dispersion (FDis) of plants was higher in shrubby patches than in the matrix (Fig. 5a), but functional evenness (FEve) was similar (Fig. 5b). These results imply that the high functional distinctiveness of shrubby patches does not arise from the presence of a few rare woody species that are absent from the matrix, but from the presence of diverse and abundant woody vegetation.

The higher plant functional diversity found in the patches, contrasts with the simpler structure of plant communities in the open matrix and contributes to increase vegetation heterogeneity in wood-pasture landscapes. This enhances niche availability by providing a range of unique microhabitats, food and breeding resources. For example, several studies have revealed a crucial role of shrubs for nesting birds (Hartel et al., 2014), reptiles (Godinho et al., 2010) and mammals (Martínez, 2009) within pastures. Furthermore, woody vegetation patches have substantial potential to alter abiotic conditions including shade, soil nutrient richness and micro-climate, that profoundly influence species composition patterns (Moreno and Pulido, 2009). For instance, a higher shrub cover increases soil moisture and promotes a higher diversity of ground-dwelling arthropods in arid landscapes (Taboada et al., 2006). Moreover, stopping grazing allows shrub regeneration and has been shown to greatly enhance fruticose lichen growth (Concostrina-Zubiri et al., 2016). Hence, it is expected that shrubby patches not only contribute towards landscape heterogeneity and plant functional diversity in wood-pastures, but also to the functional diversity of other taxonomic groups present in these habitats.

Interestingly, the observed trait-level differences of beetle and lichen assemblages did not result in distinct functional dispersion (FDis) patterns (Fig. 5a), indicating that the functional dispersion level

of the patches is similar to that of the matrix. However, in both taxa, we observed higher functional evenness (FEve) in the patches (Fig. 5b). FEve reflects how regularly the abundance of different traits is distributed across the habitat (Villéger et al., 2008). Therefore, the higher values of FEve observed for these two distinct taxa in woody vegetation patches suggests the patches provide a diversity of food resources and micro-habitats that allows for an even distribution of the various traits. On the other hand, low values of FEve may indicate an under-utilization of some of the available functional niches (Mason et al., 2005), particularly when these are evenly distributed in the habitat (Gerisch et al., 2011). Because the open matrix has a regular distribution of plant functional groups (Fig. 5b), our results suggest that the lower FEve values observed for beetles and lichens probably represent an uneven trait distribution in the matrix habitat driven by land-use (Hillebrand et al., 2008; Birkhofer et al., 2017). For example, it has been reported that habitat homogenization driven by intensive land-use may stimulate the dominance of specific traits (Hillebrand et al., 2008) and may reduce functional diversity (Mouillot et al., 2013).

Regarding functional structure, we detected that smaller beetle species are clearly more prevalent in patches than in the matrix (Fig. 3a). Higher vegetation heterogeneity in the patches may facilitate micro-habitat complexity that favours small insects. In fact, it has been shown that small-sized staphylinids are associated to more treed micro-habitats in Mediterranean habitats (García-Tejero and Taboada, 2016). Moreover, it has been reported that, after a habitat disturbance, smaller beetles tend to prefer natural remnants to early succession stages of vegetation (Cunningham and Murray, 2006). Fungivore beetles, although quite rare in our sampling, were more prevalent in the patches (Fig. 3b). Although several studies have reported a high diversity of fungi in wood-pastures (Nordén et al., 2004; Diamandis and Perlerou, 2013), in highly managed oak wood-pastures, fungi development may be to some extent restricted to relatively humid spots. That is the case of the studied patches of natural

vegetation, where dense woody cover lowers temperature, increases humidity and provides plant material left to decompose in loco, thus creating suitable conditions for fungi and for the animal species feeding on them.

Lichen communities are regarded as an ecological indicator (Ellis et al., 2007; Pinho et al., 2011) and, although there were no significant differences in FDis between patches and matrix, we observed a shift in the composition of lichen communities. Lichens present in the patches have greater preference for moister environments than those present in the matrix (Fig. 4d). In fact, patches have a higher tree and shrub density, which increases shading and evapotranspiration. Both conditions generate a micro-climatic environment with lower temperature, lower radiation and higher moisture, to which lichen communities respond (Giordani et al., 2013; Li et al., 2013). The shift in the lichen communities is also indicative of higher nutrient availability in the matrix than in the patches (Fig. 4f). Lichens in the matrix have ecological preferences for, and are more tolerant to, higher nutrient loads than those present in the patches. Several factors may contribute to a higher nutrient availability in the wood-pasture matrix, such as a lower soil cover due to grazing and shrub removal, and the dominance of annual plants, which only provide soil cover during part of the year. Together, they increase the exposure of soil in the matrix to dust particles, naturally enriched in nutrients (Pinho et al., 2008). Livestock excrements, mostly present in the matrix, also enrich the system with nutrients. Additionally, the canopy of trees in the patches may be able to intercept particles and nutrients (Santos et al., 2017). Larger lichens with higher surface exposure in relation to dry weight, which require moister conditions and tolerate less dust particles, as well as crustose lichens, which are highly resistant to light stress and have low nutrient demand due to their slow growth (Armstrong and Bradwell, 2010), are thus more abundant in patch areas. The presence of only a few scattered trees in the matrix may provide less appropriate conditions for hygrophytic (Fig. 4d), fruticose (Fig. 4a) and large foliose lichens (Fig. 4b).

In contrast, most foliose-narrow lichens tolerate nutrient-rich environments and xerophytic conditions and are thus more abundant in the matrix (Fig. 4c).

Overall, the substantial differences in the functional structure of plants reveal the traits (Fig. 2) that potentially driving the ecosystem functioning in patches and in the matrix (Grime, 1998). These differences are reflected in higher functional dissimilarity of plants indicating elevated niche differentiation compared to the matrix (Tilman, 1997). Higher niche diversity may facilitate enhanced complementary in resource use (Hooper, 1998; Díaz and Cabido, 2001) in patches, which is indicated by the functional evenness patterns of beetles and lichens in our study. Moreover, several traits of beetles and lichens contribute to distinct functional composition of patches and the matrix potentially interacting with ecosystem functioning in various levels. To conclude, our results highlight the positive influence of shrubby patches on the functional diversity of wood-pastures. However, we should note that the analysis needs to be replicated in other wood-pasture areas and with a larger sample to ensure results can be extrapolated to other similar systems.

5. Conclusions and Implications for Management

Our results indicate that shrubby patches contribute greatly to the biodiversity and ecosystem functioning of wood-pasture landscapes. We demonstrated that shrubby patches contribute to the functional diversity of these habitats, maintaining a high level of biodiversity beyond species richness. Functional diversity is important to preserve healthy and functional ecosystems (Cadotte et al., 2011) an issue that is particularly relevant for threatened wood-pasture systems (Hartel et al., 2015). For this reason, the establishment and long-term maintenance of small shrubby patches should be stimulated to preserve the High Nature Value Farmland (HNVF) status of wood-pastures.

The ensuing challenge is how to conciliate the preservation of such habitat patches in the

current scenario of increasing intensification of the use of wood-pastures observed throughout Europe, driven by ongoing market, social and environmental changes (Plieninger and Bieling, 2013). Despite their major ecological importance, shrubby patches often occupy very small areas, usually over and around small rocky outcrops. Areas with such conditions are not amenable to be actively exploited and are often not used by land managers, so maintaining shrubby patches in such conditions is likely to have little negative impact on economic productivity. Activities that have been proposed to promote woody plant regeneration, such as controlling grazing pressure or changing grazing type and timing, as well as maintaining grazing-excluded areas (Plieninger, 2007; Almeida et al., 2015), can also benefit shrubby patches. Similarly, landscape restoration schemes (Ockendon et al., 2018) could aim to actively establish small vegetation patches composed of native species. Such actions could be stimulated through policy directives or implemented as prescriptions under forest certification frameworks (Auld et al., 2008; Bugalho et al., 2011). These prescriptions, such as the set-aside areas required by the Forest Stewardship Council (FSC) certification scheme, have shown remarkable success in stimulating tree regeneration and shrub diversity in wood-pastures (Dias et al., 2014). Likewise, recommendations to maintain and promote small vegetation patches could substantially boost the functional wealth of wood-pastures at a very low implementation cost.

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Table S1: Plant cover data and abundance data of beetles and lichens.

Site	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix
Area	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	BR	BR	BR	BR	BR	BR	BR	BR
Quercus rotundifolia	62.5	2.5	37.5	2.5	0	2.5	37.5	37.5	37.5	0	0	2.5	2.5	15	2.5	0	0.1	2.5	2.5	2.5	0	0	0	0
Quercus suber	2.5	0	62.5	62.5	0	0	0	2.5	0	0	2.5	0	0	0	0	0	0	0	0	0	0	0	0	0
Olea europaea	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	62.5	62.5	62.5	37.5	0	0	0	0
Quercus coccifera coccifera	15	37.5	0	0	87.5	0	0	2.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smilax aspera	2.5	0.1	0.1	0	2.5	2.5	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryonia dioica	0	0	0	0	0	0.1	0	0.1	0	0	0	0	0	0	0	0	0.1	0	0.1	0	0	0	0	0
Rubia peregrina	0.1	0	0.1	0	0	0.1	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus ulmifolius	0.1	0	2.5	0.1	0	0	2.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnus alaternus	2.5	37.5	0.1	2.5	37.5	0	0	15	2.5	0	0	0	0	0	0	0	0	0	15	15	0	0	0	0
Pistacia lentiscus	2.5	15	0	37.5	0	62.5	15	37.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnus lycioides oleoides	0	0	0	0	0	2.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asparagus aphyllus	0	0	0	0.1	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ruscus aculeatus	2.5	0.1	2.5	37.5	0.1	0	2.5	2.5	2.5	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0
Cistus salviifolius	15	0	0	0	0.1	0.1	2.5	0	15	0	0	0	0	37.5	0	0	0.1	0.1	0.1	0	0	0	0	0
Daphne gnidium	0.1	0	0.1	0.1	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0
Calamintha nepeta nepeta	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0
Arum italicum italicum	0	0.1	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0	0	0	0
Urginea maritima	0.1	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0
Asphodelus ramosus	0	0	0	0.1	0	0	0	2.5	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0
Muscari comosum	0.1	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0.1	0.1	0	0	0	0	0	0	0	0
Polypodium cambricum cambricum	0.1	0	0.1	0	0.1	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Daucus carota	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0
Eryngium campestre	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0
Andryala integrifolia	0.1	0	0	0.1	0.1	0	0.1	0.1	0.1	0.1	2.5	0.1	0.1	15	0.1	0	0	0	0	0	0	0	0	0
Crepis vesicaria taraxacifolia	0	0	0	0	0	0.1	0.1	0	0	0	2.5	0.1	0.1	0.1	2.5	0.1	0	0	0	0	0	0	0	0
Cynara humilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5
Leontodon taraxacoides	0.1	0.1	0	0.1	0	0.1	0.1	0	0.1	0.1	0.1	0.1	0.1	0.1	87.5	0	0.1	0	0	0	0.1	37.5	0.1	0.1
Senecio jacobaea	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0
Echium plantagineum	0	0.1	0	0	0	0	0	0	0	0.1	0.1	0.1	0.1	0.1	0	0.1	0	0.1	0	0	0.1	2.5	0.1	0.1
Silene vulgaris vulgaris	2.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0.1	0	0	0	0
Umbilicus rupestris	2.5	0.1	2.5	0	0.1	0.1	0	0.1	2.5	0	0	0	0	0	0	0	2.5	0.1	0.1	0	0	0	0	0
Plantago coronopus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	0.1	0	0	0	0	0	37.5	0	0.1
Plantago lagopus	0	0	0	0	0	0.1	0	0	0	0.1	0.1	0.1	0.1	0	15	15	0	0.1	0	0	0	2.5	0	0.1
Dactylis glomerata	0.1	0	0.1	0.1	0	0	0	0	0.1	0	0.1	0.1	0.1	0.1	0	0	0.1	0	0.1	0	0	0	0	0
Digitalis purpurea	0	0	0	0	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0	0
Lotus corniculatus	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1
Trifolium repens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	0.1	0	0	0	0	0	2.5	0	0
Cynodon dactylon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.1
Holcus lanatus	0	0	0	0	0.1	0	0	0.1	0	0	0.1	0	0	0	0	0	0	0	0.1	0	0	0	0	0
Rumex acetosella angiocarpus	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0	0	0	0	0	0	0	0
Rumex pulcher woodsii	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0	0.1	0.1	0	0	0	0	0	0.1	0	0
Orobanche minor	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0	0	0	0	0	0	0	0	0	0
Carduus tenuiflorus	2.5	0.1	0	0	0	0.1	0	0.1	0.1	0	0	0	0	0	0	0.1	0.1	0	0.1	0.1	0	0	0	0
Crepis capillaris	0.1	0	0	0	0.1	0.1	0.1	0.1	0.1	2.5	2.5	2.5	2.5	0.1	0.1	15	15	0.1	0	0.1	0	0	0.1	0
Hypochaeris glabra	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	2.5	0.1	0	0	0	0	0	0.1	0	0
Sonchus oleraceus	0.1	0	0	0	0	0	0	0.1	0	0	0	0.1	0.1	0.1	0	0	0	0	0	0	0	0	0	0
Urospermum picroides	0	0	0	0	0	0	0	0.1	0.1	0	0.1	0	0	0	0	0	2.5	0	0.1	0	0	0	0	0
Sisymbrium officinale	0	0	0	0	0	0.1	0	0.1	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0
Cerastium glomeratum	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0.1	0.1	0	0	0	0	0	0	0.1	0
Polycarpon tetraphyllum tetraphyllum	0	0	0	0	0	0	0.1	0	0	0	0.1	0	0	0	0.1	0.1	0.1	0	0	0	0	0	0.1	0.1
Silene gallica	0.1	0	0	0	0	0	0.1	0	0	0	2.5	0.1	0.1	0.1	0.1	0.1	0	0	0	0	0.1	0	0.1	0
Tuberaria guttata	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0	0.1	0	0.1	0.1	0	0	0	0	0
Medicago polymorpha	0	0	0	0	0	0	0	0	0	0	2.5	0.1	0.1	0.1	2.5	0.1	0	0	0	0	0	0.1	0.1	0.1
Ornithopus compressus	0.1	0	0	0	0.1	0	2.5	0	0	0	0	0.1	0.1	2.5	2.5	0.1	0.1	0	0	0	0	0	0	0
Trifolium arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0	0	0	0	0.1	0
Trifolium glomeratum	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0.1	0
Juncus bufonius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	2.5	2.5	2.5
Juncus capitatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1
Stachys arvensis	0	0	0	0	0	0	0	0.1	0	0	0	0.1	0.1	0	15	0	0.1	0	0.1	0	0	0	0	0
Aira caryophyllea	0.1	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Avena barbata	0.1	0	0	0	0	0.1	0	0.1	15	0.1	37.5	62.5	62.5	37.5	37.5	0.1	0	0	0	0	0.1	0	0.1	0
Bromus diandrus	0	0	0.1	0	0	0	0	0	0	0.1	37.5	2.5	2.5	0.1	0	0.1	2.5	0	0.1	0.1	0	0	0	0
Bromus hordeaceus	0.1	2.5	0	0	0.1	0	0	0	0	0.1	0.1	0.1	0.1	0	2.5	2.5	0	0	0	0	0	2.5	0.1	0
Bromus madritensis	0.1	0	0	0	0.1	0.1	0	0.1	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0
Cynosurus echinatus	0.1	0	0	0	0	0.1	0	0	0.1	0	0.1	0	0	0	0	0.1	0	0	0	0	0	0	0	0
Holcus annus	0	0	0	0	0	0.1	0.1	0	0.1	0.1	0	0	0	2.5	0.1	0	0.1	0	0	0.1	0.1	0	0.1	0
Hordeum murinum	0.1	0	0	0	0	2.5	0	0.1	0	0.1	62.5	0.1	0.1	0	62.5	0.1	0.1	0	0	0	0	0	0	0
Vulpia myuros	0.1	0	0	0.1	0	0	0	0	0.1	0	0	0.1	0.1	0.1	0	0.1	0	0	0.1	0	0.1	0.1	0.1	2.5
Rumex bucephalophorus	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0.1	0.1	15	0	0	0	0	0	0	0.1	0.1
Anagallis arvensis	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0	0	0	0.1	0
Galium aparine	0	0	0.1	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0.1	0	0.1	0	0	0	0	0
Misopates orontium	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0.1	0	0	0	0	0	0	0	0	0	0
Centranthus calcitrapae	0.1	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Site	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix
Area	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	BR	BR	BR	BR	BR	BR	BR	BR
Stagetus elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	1	0	0
Ptinus fur	0	0	0	0	0	0	3	1	0	3	3	6	3	13	1	1	3	3	4	1	0	0	0	0
Omonadus floralis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Malvapion malvae	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	1
Bruchidius jocosus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1
Bruchus loti	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brachinus (Brachinoaptinus) bellicosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1
Calathus hispanicus dejeani	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Calathus (Neocalathus) granatensis	4	0	1	9	0	8	13	13	2	1	1	2	4	16	6	10	8	8	7	2	0	0	0	0
Carabus (Macrothorax) rugosus celtibericus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Carabus (Mesocarabus) lusitanicus latus	0	0	0	0	0	0	0	0	0	0	8	13	0	0	0	1	0	0	0	0	0	0	0	0
Dixus sphaerocephalus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Pterostichus (Steropus) ebenus	0	0	3	0	0	0	1	1	0	4	4	18	0	6	1	1	1	0	2	1	67	8	66	37
Trechus obtusus	2	0	1	0	5	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scymnus (Pullus) suturalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Sitona lineatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
Xyleborus monographus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Attagenus trifasciatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Attagenus unicolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	9	4
Dicronychus cinereus	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Lycoperdina bovistae	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carcinops pumilio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Hister quadrimaculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Teretrius (Neotepretius) parasita	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Catops fuscus	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lampyris iberica	0	0	0	0	4	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dorcus parallelipipedus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Meloe proscarabaeus proscarabaeus	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Serica brunea	0	1	0	0	0	0	1	0	0	0	0	0	0	5	0	1	0	0	0	0	1	1	1	1
Monotropus lusitanica	1	0	0	0	1	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	6	0	1	1
Chasmatopterus hirtulus	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paleostigus palpalis	7	6	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus (Reliconthophagus) nigellus	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0
Oryzaephylus surinamensis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
Ocypus olens olens	0	0	0	1	4	0	3	1	1	1	13	17	26	9	20	13	0	0	0	0	0	0	0	0
Alphasida marseuli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0
Sepidium bidentatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0
Tentyria platyceps	1	0	0	2	0	3	0	0	0	20	1	7	0	4	4	4	5	0	6	0	10	0	1	1
Akis granulifera	0	0	0	6	4	0	10	3	0	6	0	18	0	0	5	0	0	0	0	0	0	0	0	0
Akis lusitanica	6	2	0	4	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Blaps lusitanica	0	1	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4
Blaps gigas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Trox perlatus hispanicus	0	0	0	1	0	2	3	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1

Site	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Matrix	Ungrazed patch	Ungrazed patch	Ungrazed patch	Ungrazed patch	Matrix	Matrix	Matrix	Matrix
Area	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	FM	BR	BR	BR	BR	BR	BR	BR	BR
Agonimia octospora	12	0	0	0	0	0	0	0	0	27	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Agonimia opuntiella	0	0	3	0	2	0	0	0	0	0	4	11	3	0	22	0	1	0	12	0	0	0	4	1
Agonimia tristicula	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1
Alyxoria varia	1	0	0	0	0	0	0	0	0	0	4	2	1	0	0	0	0	2	2	0	2	3	0	0
Bacidia circumspecta	0	0	4	0	0	2	0	0	0	1	0	5	1	0	3	0	0	2	1	0	0	0	0	0
Bacidia iberica	0	0	1	0	0	1	1	0	4	1	0	4	0	0	0	0	0	0	1	0	0	0	0	0
Bacidia punica	0	0	0	0	0	0	0	0	0	0	3	0	4	0	0	0	0	0	0	0	0	0	0	0
Caloplaca ferruginea	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caloplaca ulcerosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Collema furfuraceum	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collema flaccidum	4	0	5	5	3	0	12	3	6	13	1	9	10	8	18	5	8	4	4	14	8	1	8	12
Collema ryssoleum	0	0	0	2	0	0	1	0	4	1	0	3	0	0	1	0	0	0	0	0	0	0	0	0
Dendrographa decolorans	0	1	0	0	0	0	0	0	0	1	0	0	3	0	0	2	1	0	0	1	7	5	0	0
Evernia prunastri	0	9	5	5	0	0	2	0	21	6	0	0	2	4	0	0	0	12	4	19	0	0	0	0
Flavoparmelia caperata	13	50	10	24	0	8	5	3	13	11	0	0	10	1	5	0	0	13	11	11	1	0	0	4
Hyperphyscia adglutinata	0	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lecanora albella	0	11	3	9	0	5	0	2	6	1	0	0	0	0	0	0	0	10	0	13	0	0	0	0
Lecanora chlarotera	0	7	6	4	0	0	0	4	2	0	0	1	3	0	0	1	0	0	0	1	0	0	0	3
Leptogium brebissonii	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
Leptogium subtile	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	5	0	12	0	0	0	0	0
Normandina pulchella	0	4	3	0	0	0	0	5	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ochrolechia pallescens	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0
Parmelia sulcata	0	8	15	5	0	2	0	1	14	0	0	0	1	0	0	0	0	7	20	9	0	0	0	3
Parmelina tiliacea	5	3	3	3	0	2	5	1	1	1	0	7	5	4	0	0	7	2	0	2	11	4	0	0
Parmotrema hypoleucinum	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parmotrema perlatum	13	40	22	24	0	11	6	8	13	14	0	2	18	13	0	2	0	0	4	0	4	0	0	12
Pertusaria albescens	0	0	0	0	0	3	0	0	0	0	9	8	0	0	0	13	0	5	0	0	0	0	0	4
Pertusaria amara	13	26	32	16	3	4	4	11	31	23	2	5	25	32	11	3	10	22	11	36	29	8	2	16
Pertusaria coccodes	1	3	0	2	0	0	0	2	0	2	0	2	0	4	1	0	5	4	1	1	2	0	0	0
Pertusaria flavida	0	0	2	0	0	0	0	0	0	0	0	6	1	1	0	0	2	0	0	4	0	0	0	0
Pertusaria heterochroa	0	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0
Pertusaria pertusa	1	1	5	0	0	1	0	2	2	1	0	0	1	1	0	3	5	4	0	3	1	0	0	1
Phaeophyscia cernohorsky	0	0	0	0	0	0	0	0	0	5	6	0	0	2	1	0	0	0	0	0	0	0	0	0
Phaeophyscia orbicularis	3	0	1	0	10	15	3	0	0	1	5	11	1	12	2	56	0	2	2	2	15	0	0	0
Phlyctis agelaea	5	14	10	3	0	0	0	5	1	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0
Phlyctis argena	28	41	40	27	4	5	0	26	19	7	9	5	30	21	7	15	7	13	20	29	6	3	0	3
Physcia adscendens	2	20	27	3	0	0	9	14	19	8	0	10	36	17	2	6	2	6	2	3	9	1	9	10
Physcia stellaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Physcia tenella	1	0	7	0	0	0	1	0	0	0	0	0	6	3	0	0	2	0	0	6	60	0	14	30
Physciella chloantha	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Physconia enteroxantha	0	0	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0	0	0	0	0	40	0	0
Porina aenea	2	10	10	0	0	0	2	0	0	6	2	0	0	0	3	0	0	0	0	0	0	1	0	0
Punctelia subrudecta	0	2	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyrrhospora quernea	0	5	5	7	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0
Ramalina canariensis	0	1	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	5	1	0	0
Ramalina farinacea	7	43	22	19	0	7	2	4	10	12	1	1	9	4	0	3	4	18	20	17	0	0	0	0
Ramalina fastigiata	0	4	3	0	0	0	0	0	0	4	0	0	14	1	0	1	0	0	0	0	3	0	0	0
Ramalina fraxinea	0	0	0	0	0	0	0	3	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rinodina capensis	0	0	13	0	0	0	2	0	9	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0
Rinodina oleae	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ramalina subgeniculata	1	11	20	0	0	3	1	0	5	0	0	0	14	0	0	0	3	5	12	12	0	0	0	0
Trapeliopsis flexuosa	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0
Usnea rubicunda	4	23	0	11	0	0	0	1	2	0	0	0	0	0	0	0	0	4	0	2	0	0	0	0
Varicellaria hemisphaerica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0
Waynea stoechadiana	29	0	5	12	3	3	8	19	1	20	12	9	7	5	21	7	16	3	15	20	15	0	11	7
Xanthoria parietina	0	0	0	0	0	0	0	2	0	0	0	0	6	0	0	1	0	0	0	0	1	0	0	0
Zwackhia viridis	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S2: Trait data of plants, beetles and lichens.

Species	Leaf phenology	Leaf shape	Fruit type	Growth form	Woodiness	Dispersal strategy.Zoochory	Dispersal strategy.Allochory	Dispersal strategy.Autochory
Quercus rotundifolia	Evergreen	Broad	Dry	Tree	Woody	1	0	0
Quercus suber	Evergreen	Broad	Dry	Tree	Woody	1	0	0
Olea europaea	Evergreen	Broad	Fleshy	Tree	Woody	1	0	0
Quercus coccifera coccifera	Evergreen	Broad	Dry	Tree	Woody	1	0	0
Smilax aspera	Evergreen	Broad	Fleshy	Shrub	Woody	1	0	0
Bryonia dioica	Evergreen	Broad	Fleshy	Shrub	Non-woody	0	1	0
Rubia peregrina	Evergreen	Broad	Fleshy	Shrub	Non-woody	1	0	0
Rubus ulmifolius	Evergreen	Broad	Fleshy	Shrub	Woody	1	0	0
Rhamnus alaternus	Evergreen	Broad	Fleshy	Shrub	Woody	1	0	0
Pistacia lentiscus	Evergreen	Linear	Fleshy	Shrub	Woody	1	0	0
Rhamnus lycioides oleoides	Evergreen	Broad	Fleshy	Shrub	Woody	1	0	0
Asparagus aphyllus	Evergreen	Linear	Fleshy	Shrub	Woody	1	0	0
Ruscus aculeatus	Evergreen	Broad	Fleshy	Shrub	Woody	1	0	0
Cistus salviifolius	Deciduous	Broad	Dry	Shrub	Woody	0	0.5	0.5
Daphne gnidium	Evergreen	Linear	Fleshy	Shrub	Woody	1	0	0
Calamintha nepeta nepeta	Deciduous	Broad	Dry	Shrub	Woody	0	0	1
Arum italicum italicum	Deciduous	Broad	Fleshy	Herb	Non-woody	0	1	0
Urginea maritima	Deciduous	Broad	Dry	Herb	Non-woody	0.3	0.3	0.3
Asphodelus ramosus	Deciduous	Linear	Dry	Herb	Non-woody	0	0	1
Muscari comosum	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Polypodium cambricum cambricum	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Daucus carota	Deciduous	Broad	Dry	Herb	Non-woody	0.5	0.5	0
Eryngium campestre	Deciduous	Broad	Dry	Herb	Non-woody	0	0.5	0.5
Andryala integrifolia	Deciduous	Linear	Dry	Herb	Non-woody	0	0	1
Crepis vesicaria taraxacifolia	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Cynara humilis	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Leontodon taraxacoides	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Senecio jacobaea	Deciduous	Linear	Dry	Herb	Non-woody	0	0.5	0.5
Echium plantagineum	Deciduous	Linear	Dry	Herb	Non-woody	0.5	0.5	0
Silene vulgaris vulgaris	Deciduous	Linear	Dry	Herb	Non-woody	0	0.5	0.5
Umbilicus rupestris	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Plantago coronopus	Deciduous	Linear	Dry	Herb	Non-woody	0	0.5	0.5
Plantago lagopus	Deciduous	Linear	Dry	Herb	Non-woody	0.5	0.5	0
Dactylis glomerata	Deciduous	Linear	Dry	Herb	Non-woody	0	0.5	0.5
Digitalis purpurea	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Lotus corniculatus	Deciduous	Linear	Dry	Herb	Non-woody	0	0	1
Trifolium repens	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Cynodon dactylon	Deciduous	Linear	Dry	Graminoid	Non-woody	0	1	0
Holcus lanatus	Deciduous	Broad	Dry	Graminoid	Non-woody	0	1	0
Rumex acetosella angiocarpus	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Rumex pulcher woodsii	Deciduous	Linear	Dry	Herb	Non-woody	1	0	0
Orobanche minor	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Carduus tenuiflorus	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Crepis capillaris	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Hypochaeris glabra	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Sonchus oleraceus	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Urospermum picroides	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Sisymbrium officinale	Deciduous	Linear	Dry	Herb	Non-woody	0	0.5	0.5
Cerastium glomeratum	Deciduous	Broad	Dry	Herb	Non-woody	0	0.5	0.5
Polycarpon tetraphyllum tetraphyllum	Deciduous	Broad	Dry	Herb	Non-woody	0	0.5	0.5
Silene gallica	Deciduous	Linear	Dry	Herb	Non-woody	0	0.5	0.5
Tuberaria guttata	Deciduous	Linear	Dry	Herb	Non-woody	0	0	1
Medicago polymorpha	Deciduous	Broad	Dry	Herb	Non-woody	1	0	0
Ornithopus compressus	Deciduous	Broad	Dry	Herb	Non-woody	0	0	1
Trifolium arvense	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Trifolium glomeratum	Deciduous	Broad	Dry	Herb	Non-woody	1	0	0
Juncus bufonius	Deciduous	Linear	Dry	Graminoid	Non-woody	1	0	0
Juncus capitatus	Deciduous	Linear	Dry	Graminoid	Non-woody	1	0	0
Stachys arvensis	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0
Aira caryophyllea	Deciduous	Linear	Dry	Graminoid	Non-woody	0	1	0
Avena barbata	Deciduous	Linear	Dry	Graminoid	Non-woody	0	1	0
Bromus diandrus	Deciduous	Linear	Dry	Graminoid	Non-woody	1	0	0
Bromus hordeaceus	Deciduous	Broad	Dry	Graminoid	Non-woody	0	1	0
Bromus madritensis	Deciduous	Broad	Dry	Graminoid	Non-woody	0	1	0
Cynosurus echinatus	Deciduous	Linear	Dry	Graminoid	Non-woody	0	1	0
Holcus annus	Deciduous	Linear	Dry	Graminoid	Non-woody	0.3	0.3	0.3
Hordeum murinum	Deciduous	Linear	Dry	Graminoid	Non-woody	0.5	0.5	0
Vulpia myuros	Deciduous	Linear	Dry	Graminoid	Non-woody	0	1	0
Rumex bucephalophorus	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Anagallis arvensis	Deciduous	Broad	Dry	Herb	Non-woody	0	0	1
Galium aparine	Deciduous	Linear	Dry	Herb	Non-woody	0	1	0
Misopates orontium	Deciduous	Linear	Dry	Herb	Non-woody	0	0.5	0.5
Centranthus calcitrapae	Deciduous	Broad	Dry	Herb	Non-woody	0	1	0

Species	Dispersal strategy	Body size (mm)	Feeding guild
Stagetus elongatus	Macropterous	1.9	Saprovore
Ptinus fur	Macropterous	2.1	Saprovore
Omonadus floralis	Macropterous	2.8	Herbivore
Malvapion malvae	Macropterous	2.1	Herbivore
Bruchidius jocosus	Macropterous	2	Herbivore
Bruchus loti	Macropterous	3	Herbivore
Brachinus (Brachinoaptinus) bellicosus	Brachypterous	8	Predator
Calathus hispanicus dejeani	Brachypterous	12.5	Predator
Calathus (Neocalathus) granatensis	Brachypterous	10.5	Predator
Carabus (Macrothorax) rugosus celtibericus	Brachypterous	33.5	Predator
Carabus (Mesocarabus) lusitanicus latus	Brachypterous	21	Predator
Dixus sphaerocephalus	Macropterous	6.5	Herbivore
Pterostichus (Steropus) ebenus	Brachypterous	18	Predator
Trechus obtusus	Macropterous	3.6	Predator
Scymnus (Pullus) suturalis	Macropterous	2.5	Predator
Sitona lineatus	Macropterous	4.15	Herbivore
Xyleborus monographus	Dimorphic	2.3	Herbivore
Attagenus trifasciatus	Macropterous	3.8	Saprovore
Attagenus unicolor	Macropterous	5	Saprovore
Dicronychus cinereus	Macropterous	6.5	Herbivore
Lycoperdina bovistae	Brachypterous	4	Fungivore
Carcinops pumilio	Macropterous	1.15	Predator
Hister quadrimaculatus	Macropterous	6.75	Saprovore
Teretrius (Neotepretius) parasita	Macropterous	3	Saprovore
Catops fuscus	Macropterous	2	Predator
Lampyris iberica	Dimorphic	11	Predator
Dorcus parallelipipedus	Macropterous	2.75	Herbivore
Meloe proscarabaeus proscarabaeus	Brachypterous	25	Herbivore
Serica brunea	Macropterous	11	Herbivore
Monotropus lusitanica	Macropterous	10.25	Herbivore
Chasmatopterus hirtulus	Macropterous	6.75	Herbivore
Paleostigus palpalis	Brachypterous	4.85	Predator
Onthophagus (Reliconthophagus) nigellus	Macropterous	4	Saprovore
Oryzaephylus surinamensis	Macropterous	2.75	Herbivore
Ocypus olens olens	Macropterous	18.5	Predator
Alphasida marseuli	Brachypterous	14	Fungivore
Sepidium bidentatum	Brachypterous	17.5	Fungivore
Tentyria platyceps	Brachypterous	13.3	Fungivore
Akis granulifera	Brachypterous	22.5	Fungivore
Akis lusitanica	Brachypterous	20	Fungivore
Blaps lusitanica	Brachypterous	18.5	Fungivore
Blaps gigas	Brachypterous	24	Fungivore
Trox perlatus hispanicus	Brachypterous	5.5	Saprovore

Species	Growth form	Photobiont type	Reproduction strategy	Eutrofication tolerance	Humidity preference
Agonimia octospora	Squamulose	Chloroccocoid	Sexual	Oligotrophic	Hygrophytic
Agonimia opuntiella	Squamulose	Chloroccocoid	Sexual	Mesotrophic	Mesophytic
Agonimia tristicula	Squamulose	Chloroccocoid	Sexual	Oligotrophic	Mesophytic
Alyxoria varia	Crustose	Trentepohlia	Sexual	Oligotrophic	Mesophytic
Bacidia circumspecta	Crustose	Chloroccocoid	Sexual	Mesotrophic	Hygrophytic
Bacidia iberica	Crustose	Chloroccocoid	Sexual	Oligotrophic	Hygrophytic
Bacidia punica	Crustose	Chloroccocoid	Sexual	Oligotrophic	Hygrophytic
Caloplaca ferruginea	Crustose	Chloroccocoid	Sexual	Mesotrophic	Mesophytic
Caloplaca ulcerosa	Crustose	Chloroccocoid	Asexual sorediate	Nitrophytic	Xerophytic
Collema furfuraceum	Foliose broad-lobed	Cyanolichens	Asexual isidiate	Mesotrophic	Hygrophytic
Collema flaccidum	Foliose broad-lobed	Cyanolichens	Asexual isidiate	Oligotrophic	Hygrophytic
Collema ryssoleum	Foliose broad-lobed	Cyanolichens	Sexual	Oligotrophic	Mesophytic
Dendrographa decolorans	Crustose	Trentepohlia	Asexual sorediate	Mesotrophic	Hygrophytic
Evernia prunastri	Fruticose	Chloroccocoid	Asexual sorediate	Mesotrophic	Mesophytic
Flavoparmelia caperata	Foliose broad-lobed	Chloroccocoid	Asexual sorediate	Mesotrophic	Mesophytic
Hyperphyscia adglutinata	Foliose narrow-lobed	Chloroccocoid	Asexual sorediate	Nitrophytic	Xerophytic
Lecanora albella	Crustose	Chloroccocoid	Sexual	Oligotrophic	Hygrophytic
Lecanora chlarotera	Crustose	Chloroccocoid	Sexual	Nitrophytic	Xerophytic
Leptogium brebissonii	Foliose broad-lobed	Cyanolichens	Asexual isidiate	Oligotrophic	Hygrophytic
Leptogium subtile	Squamulose	Cyanolichens	Sexual	Mesotrophic	Mesophytic
Normandina pulchella	Squamulose	Chloroccocoid	Asexual sorediate	Mesotrophic	Mesophytic
Ochrolechia pallescens	Crustose	Chloroccocoid	Sexual	Oligotrophic	Mesophytic
Parmelia sulcata	Foliose broad-lobed	Chloroccocoid	Asexual sorediate	Mesotrophic	Mesophytic
Parmelina tiliacea	Foliose broad-lobed	Chloroccocoid	Asexual isidiate	Mesotrophic	Mesophytic
Parmotrema hypoleucinum	Foliose broad-lobed	Chloroccocoid	Asexual sorediate	Oligotrophic	Hygrophytic
Parmotrema perlatum	Foliose broad-lobed	Chloroccocoid	Asexual sorediate	Oligotrophic	Mesophytic
Pertusaria albescens	Crustose	Chloroccocoid	Asexual sorediate	Mesotrophic	Mesophytic
Pertusaria amara	Crustose	Chloroccocoid	Asexual sorediate	Mesotrophic	Mesophytic
Pertusaria coccodes	Crustose	Chloroccocoid	Asexual isidiate	Mesotrophic	Hygrophytic
Pertusaria flavida	Crustose	Chloroccocoid	Asexual sorediate	Oligotrophic	Hygrophytic
Pertusaria heterochroa	Crustose	Chloroccocoid	Sexual	Mesotrophic	Mesophytic
Pertusaria pertusa	Crustose	Chloroccocoid	Sexual	Oligotrophic	Mesophytic
Phaeophyscia cernohorsky	Foliose narrow-lobed	Chloroccocoid	Asexual sorediate	Nitrophytic	Xerophytic
Phaeophyscia orbicularis	Foliose narrow-lobed	Chloroccocoid	Asexual sorediate	Nitrophytic	Xerophytic
Phlyctis agelaea	Crustose	Chloroccocoid	Sexual	Oligotrophic	Mesophytic
Phlyctis argena	Crustose	Chloroccocoid	Asexual sorediate	Oligotrophic	Mesophytic
Physcia adscendens	Foliose narrow-lobed	Chloroccocoid	Asexual sorediate	Nitrophytic	Xerophytic
Physcia stellaris	Foliose narrow-lobed	Chloroccocoid	Sexual	Nitrophytic	Mesophytic
Physcia tenella	Foliose narrow-lobed	Chloroccocoid	Asexual sorediate	Nitrophytic	Xerophytic
Physciella chloantha	Foliose narrow-lobed	Chloroccocoid	Asexual sorediate	Nitrophytic	Mesophytic
Physconia enteroxantha	Foliose narrow-lobed	Chloroccocoid	Asexual sorediate	Nitrophytic	Mesophytic
Porina aenea	Crustose	Trentepohlia	Sexual	Oligotrophic	Mesophytic
Punctelia subrudecta	Foliose broad-lobed	Chloroccocoid	Asexual sorediate	Mesotrophic	Mesophytic
Pyrrhospora quernea	Crustose	Chloroccocoid	Asexual sorediate	Mesotrophic	Hygrophytic
Ramalina canariensis	Fruticose	Chloroccocoid	Asexual sorediate	Nitrophytic	Hygrophytic
Ramalina farinacea	Fruticose	Chloroccocoid	Asexual sorediate	Oligotrophic	Hygrophytic
Ramalina fastigiata	Fruticose	Chloroccocoid	Sexual	Mesotrophic	Mesophytic
Ramalina fraxinea	Fruticose	Chloroccocoid	Sexual	Mesotrophic	Mesophytic
Rinodina capensis	Crustose	Chloroccocoid	Sexual	Oligotrophic	Mesophytic
Rinodina oleae	Crustose	Chloroccocoid	Sexual	Mesotrophic	Xerophytic
Ramalina subgeniculata	Fruticose	Chloroccocoid	Sexual	Oligotrophic	Hygrophytic
Trapeliopsis flexuosa	Crustose	Chloroccocoid	Sexual	Oligotrophic	Xerophytic
Usnea rubicunda	Fruticose	Chloroccocoid	Asexual sorediate	Oligotrophic	Hygrophytic
Varicellaria hemisphaerica	Crustose	Chloroccocoid	Asexual sorediate	Oligotrophic	Mesophytic
Waynea stoechadiana	Squamulose	Chloroccocoid	Sexual	Mesotrophic	Mesophytic
Xanthoria parietina	Foliose narrow-lobed	Chloroccocoid	Sexual	Nitrophytic	Xerophytic
Zwackhia viridis	Crustose	Trentepohlia	Sexual	Oligotrophic	Hygrophytic

Table S3. Plant, beetle and lichen trait data information.

Taxa	Traits	Trait attributes	References
Plants	Woodiness	Differences in grazing intensity	(Diaz et al. 2007)
	Growth form		(Diaz et al. 2007)
	Leaf shape		(Saatkamp et al. 2010)
	Leaf phenology		(Pakeman 2004)
	Fruit type		(Peco et al. 2012)
	Dispersal strategy		(Wesuls et al. 2012)
Beetles	Body length	The type and amount of resource use Habitat occupation	(Homburg et al. 2014) (Moretti et al. 2017)
	Feeding guild	Diet preferences Habitat use	(Homburg et al. 2014) (Moretti et al. 2017)
	Hind wing development	Dispersal ability	(Homburg et al. 2014)
Lichens	Growth form	Resource acquisition	(Asplund and Wardle 2016) (Giordani et al. 2012)
	Photobiont type	Nutrient and water uptake Aridity level of the habitat	(Matos et al. 2015)
	Reproduction strategy	Dispersal ability	(Giordani et al. 2012)
	Humidity preference	Humidity/shade rate of the habitat	(Asplund and Wardle 2016)
	Eutrophication tolerance	Resource acquisition	(Pinho et al. 2008)

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CHAPTER 4

Bird taxonomic and functional responses to decreasing management intensity in wood-pastures

To be submitted to Forest Ecology and Management:

Oksuz, D.P., Palmeirim, J.M., Correia R.A. **Bird taxonomic and functional responses to decreasing management intensity in wood-pastures.**

Abstract

Wood-pastures are socio-ecological systems covering vast areas in Europe and other temperate regions. Although used for grazing and production of various forest goods, wood-pastures harbour a rich biodiversity and are usually considered as High Nature Value Farmland. However, these valuable landscapes are threatened by the transformation from multi-functional, heterogeneous habitats to homogeneous areas due to either intensification or land abandonment, resulting from socio-economic pressures. We investigated how changes in habitat structure, representing a management intensity gradient ranging from active management to land abandonment, influence taxonomic (species richness and Shannon–Wiener diversity indices) as well as functional diversity (functional richness, functional dispersion, functional evenness indices) and functional composition (community weighted means index) of birds analysing multiple response-effect traits across Iberian Peninsula and North Africa wood-pastures. We tested the relation between each index and the management intensity gradient using generalized linear models. In contrast to species richness and diversity, functional diversity and functional composition of birds substantially responded to the changes in habitat structure. Functional richness showed a nearly-significant decline with the reduction of management intensity, resulting in higher shrub cover and height but lower habitat heterogeneity, while functional dispersion and functional evenness decreased significantly towards these shrub-dominated and less heterogeneous areas. Moreover, we observed declines in community weighted means of grassland and generalist species and in the associated ecological guilds such as granivores, ground-nesters and ground foraging species towards less managed areas. On the other hand, shrub-dominated areas favoured forest species particularly understory/canopy foragers and arboreal nesters, although the forest guild can still benefit from actively managed, heterogeneous areas. We also observed higher prevalence of birds with a lower

wing aspect ratio in less heterogeneous areas with higher tree density and fewer shrubs. Overall, our results indicate that the abandonment of wood-pastures affects the relative abundance of grassland and generalist species and the associated life-history traits leads to functional diversity loss and potentially reduced ecosystem functioning. We suggest that active management is needed to maintain spatial heterogeneity and canopy openness, enhancing trait-level response diversity and ecosystem functioning in Mediterranean wood-pastures.

Keywords: functional diversity; breeding birds; wood-pasture; management intensity; montado/dehesa

1. Introduction

Wood-pastures are social-ecological landscapes that have been shaped by various land-use regimes prevailing in much of Europe (Hartel and Plieninger 2014; Bugalho et al., 2009). These landscapes usually have high economic value provided by a multi-functional management that may include livestock grazing, cork extraction, timber production, crop cultivation and pruning for firewood and charcoal (Moreno et al., 2018). Many wood-pastures are considered High Nature Value Farmlands (HNVF), as they often conciliate economic value with the maintenance of a rich biodiversity (Andersen et al., 2003; Pinto-Correia and Ribeiro, 2012). This richness is particularly evident in wood-pasture landscapes that are spatially heterogeneous due to the presence of habitats such as riparian galleries, hedgerows, ungrazed patches and olive orchards (Graham et al., 2018; Silva et al., 2011; Leal et al., 2016; Erdõs et al., 2018b). However, due to their anthropogenic origin, the persistence and maintenance of wood-pastures and their multiple values depend on a balanced management of the landscape (Uytvanck and Verheyen, 2014; Plieninger et al., 2015). Recent social and economic changes in Europe are causing traditional forms of wood-pasture management to be replaced by contrasting

land-use trajectories towards either intensification or land abandonment (Stoate et al., 2009; Chételat et al., 2013; Bergmeier and Roellig, 2014), putting the balance between natural and economic values at risk.

Land-use intensification, fuelled by population growth and associated production demands (Krausmann et al., 2013), is known to induce habitat homogenization and cause substantial biodiversity loss (Flynn et al., 2009; Newbold et al., 2015; Gossner et al., 2016; Jeliazkov et al., 2016). On the other hand, land abandonment has also affected many wood-pastures, although its consequences are less studied than those of intensification (Cramer et al., 2008; Fonderflick et al., 2010; Estel et al., 2015). Land abandonment often leads to areas with little management beyond the use for extensive grazing or even a complete ceasing of land-use, resulting in less heterogeneous habitats with a dense shrubby vegetation (MacDonald et al., 2000; Rey Benayas et al., 2010). Studies focusing on triggers and causes of land abandonment reveal that it is particularly common in isolated mountainous regions and in unproductive areas where soil quality, water limitations and climatic factors may interact to impose substantial constraints to agricultural production or livestock grazing (Rey Benayas et al., 2007). Furthermore, socio-economic factors such as changing market values of commercial products such as cork and the decoupling of crop payments from production levels, especially in small and low-income farms, are also important drivers of traditional management abandonment in wood-pastures (Hatna and Bakker, 2011; Beilin et al., 2014; Levers et al., 2018).

The changes in habitat structure resulting from land-use abandonment usually influence biodiversity and ecosystem processes, although the effects can vary greatly depending on the taxon and geographical region evaluated (Suarez-Seoane et al., 2002; Queiroz et al., 2014). For instance, higher species diversity due to the presence of more suitable habitats (Sebek et al., 2015) as well as elevated carbon sequestration (Kuemmerle et al., 2011; Eldridge et al., 2011) and water regulation (Rey Benayas

et al., 2007) were reported as a consequence of reduced land-use intensity. However, the response of species to land abandonment vary, and while some gain from it others are negatively affected (Sebek et al., 2015; Horák et al., 2018a). For instance, lack of management may induce the loss of spatial habitat heterogeneity level of wood-pastures, for example when it is observed in olive orchards (Duarte et al. 2008) or it may reduce the overall open habitat presence that finally influence the availability of feeding and nesting resources for several species (Benton et al., 2003; Perovic et al., 2015; Sirami et al., 2009).

Changes in land-use from active management to land abandonment may influence not only species-level diversity but also the trait composition of biological communities, potentially affecting ecosystem functioning and services (Hooper et al., 2005; ; Wood et al., 2015). The life-history characteristics of individuals, namely functional traits, link species to the ecosystem and can help to reveal the mechanisms driving morphological, physiological or behavioural responses of species to changes in the environment (Díaz and Cabido, 2001). Thus, measuring how functional "response and effect traits" (i.e. traits that both influence species responses to the environment and the provision of specific services; Díaz et al., 2013; Luck et al., 2012; Hevia et al., 2016) respond to changes in habitat structure driven by land abandonment has great potential to reveal how biodiversity and ecosystem functions may be affected by this type of land use change (Mouillot et al., 2013). This knowledge is crucial to inform managers and decision-makers about potentially negative consequences of such changes and to develop adequate strategies to minimize them (Lindenmayer et al., 2008; Wood et al., 2015; Chapin et al., 2000).

Due to their ecological characteristics, birds are often regarded as a good indicator group to evaluate

how species and traits respond to environmental changes (Sekercioglu, 2006; Hartel et al., 2014). Birds are relatively conspicuous, and thus easy to monitor, and are highly mobile which allows them to respond more quickly to changes in the habitat than other less mobile taxa (Lundberg and Moberg, 2003). They also occupy high levels of the food chain, making them susceptible to changes in other groups such as plants and insects on which most of them feed (Ceia and Ramos, 2016; Sekercioglu, 2006). In wood-pastures, bird assemblages are usually diverse (Tellería, 2001; Hartel et al., 2014), and many species perform key services such as seed dispersal, pest regulation or pollination (Pons and Pausas, 2007; Whelan et al., 2008; Sekercioglu, 2012). The diverse avifauna supported by wood-pastures depends on the maintenance of a complex vegetation structure in these ecosystems and there is strong evidence that the loss of spatial habitat heterogeneity often leads to a decrease in bird species diversity (Martins et al. 2014; Ehlers Smith et al., 2015; Suri et al., 2017).

In this study, we aimed to explore how changes in habitat structure driven by different management practices influence bird taxonomic diversity, functional diversity and trait assemblages in wood-pastures across the Iberian Peninsula and North Africa. We characterized habitat structure using a set of variables including understory cover and height, tree density and habitat heterogeneity as indicators of a management intensity gradient ranging from active management to land abandonment. Specifically, we aimed to answer the following questions: i) How do changes in habitat structure influence the taxonomic and functional diversity of birds in wood-pastures? ii) Which specific traits drive the observed responses of birds to habitat along the management intensity gradient?

2. Materials and Methods

2.1. Study Area

Our study encompassed much of Portugal, Spain and Morocco, in areas dominated by a wood-pasture

system widely distributed across the western Mediterranean, known as *montado* in Portugal, *dehesa* in Spain (*dehesa*) and *azaghar* in some regions of North Africa (Fig. 1). The woody plant composition of the sampled areas is dominated by cork oak (*Quercus suber*), sometimes co-occuring with other oaks (e.g. Algerian oak *Q. canarensis*, holm oak (*Q. rotundifolia*, Pyrenean oak *Q. pyrenaica*) or pine trees (e.g. stone pine *Pinus pinea*, maritime pine *P. pinaster*). Other common tree or shrub species include mastic tree (*Pistacia lentiscus*), wild olive trees (*Olea europaea* var. *sylvestris*), strawberry tree (*Arbutus unedo*), broom (*Cytisus* spp. and *Retama* spp.), buckthorn (*Rhamnus alaternus*), elmleaf blackberry (*Rubus ulmifolius*), rockrose (*Cistus* spp.), tree heath (*Erica arborea*), lavender (*Lavandula* spp.), myrtle (*Myrtus* spp.), gorse (*Ulex* spp.) and hawthorn (*Crataegus monogyna*). In North Africa, endemic pear (*Pyrus bourgaeana* subsp. *Mamorensis*) and argan (*Argania spinosa*) trees are also present in wood-pastures.

The most common management practices in the study area are livestock grazing (cattle, sheep and pig) with various degrees of intensity, cork extraction, cropping and pruning (Moreno et al., 2018). Although less common, other traditional human-uses such as the collection of mushrooms, honey, pine nuts and medicinal plants occur in some regions of Iberian Peninsula and, more commonly, in North Africa (Berrahmouni et al., 2007; Moreno and Pulido, 2009; Sá-Sousa, 2014). Moderate to intensive grazing is prevalent in lowland wood-pastures, whereas shrub encroachment tends to occur in more rugged areas (Bugalho et al., 2009; Bugalho et al., 2011). The annual average temperature ranges between 11-18°C and the annual rainfall is 410-910 mm in the study area (http://www.worldclim.org/).

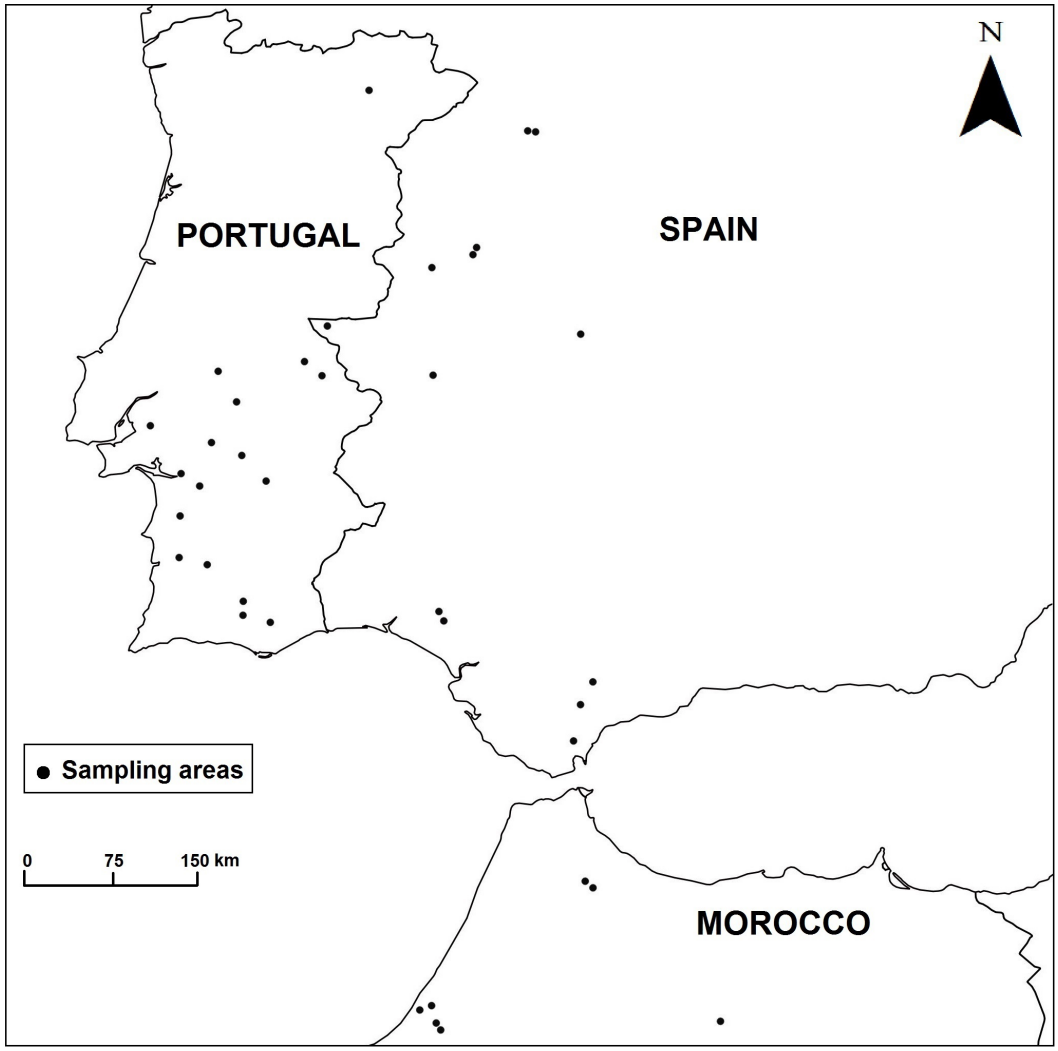

Fig. 1. Map of the study area showing the sampled wood-pastures in Portugal (N=17), Spain (N=13) and in North Africa (N=7).

2.2. Bird sampling

Bird sampling was performed during the spring of 2011 using five-minute bird point counts (Sutherland et al., 2004; Bibby et al., 2005). In total, thirty-seven wood-pastures, which had a minimum size of 50 hectares and were at least 10 km apart from each other, were sampled across the Iberian Peninsula (17 in Portugal, 13 in Spain) and North Africa (7 in Morocco). We were able to investigate

the biodiversity patterns of birds across Europe and North Africa given the information revealing the similarity of the bird species assemblages in both Europe and North Africa wood-pastures (Correia et al. 2015a). Fifteen sampling stations were set up in each of these wood-pasture areas, distancing at least 200 m from each other and 100 m or more from the wood-pasture edge. Each sampling station was visited twice, once during the early half (1 April to 15 May) and once during the late half (16 May to 20 June) of the breeding season. The same observer performed all the counts, always during periods of peak bird activity (one visit in the morning and one visit in the late afternoon for each area) and avoiding rainy and windy conditions (Sutherland et al., 2004). Areas recently harvested for cork were avoided since some species are known to be sensitive to debarking (Godinho and Rabaça, 2011; Leal et al., 2011). All the birds detected visually or acoustically were recorded and their distance to the observer was estimated. Birds detected more than 100 m away from the observer and over-flying birds were excluded from the analysis since they may not be associated with the studied habitat. The total abundance of each species in each area was defined as the maximum sum of individuals detected in the fifteen counting stations for any of the two visits, as this represents the minimum number of birds present in the wood-pasture area (Bibby et al., 2005). Bird abundance data is presented in S1 Table.

2.3. Trait data

We obtained data on six response and effect traits (Hevia et al., 2016; Luck et al., 2012) for 54 recorded species to analyse the functional diversity and functional composition of bird assemblage. The traits considered for analysis include: feeding guild, foraging strata, nest type, habitat guild, wing aspect ratio and body mass (Table 1). All trait data is listed in S2 Table.

Feeding guild: We used information on breeding season diets from Cramp and Simmons (2006) and Storchová et al. (2018) to classify species into three feeding guild categories: granivores, omnivores

and insectivores. Dietary preferences are related to the feeding ecology of species and are known to respond to habitat structure (Tscharntke et al., 2008). For example, we would expect species that feed on plants and seeds prefer open managed habitats (Leal et al., 2019; Santana et al., 2012). Conversely, we expect species that feed on fruits and insects to be more abundant in abandoned areas, where woody vegetation is usually more abundant (Santana et al., 2012; Correia et al., 2015b; De la Montaña et al., 2006).

Foraging strata: We obtained data on the percentage use of different foraging strata from the EltonTraits 1.0 database (Wilman et al., 2014). We considered four strata of resource acquisition (ground, understory, mid-high and canopy) and the relative usage of the different strata reflects the specialization level of birds among different vegetation layers (Martin and Possingham, 2005). We expect ground-foraging species to be less abundant in shrub-dominated, closed habitats (Leal et al., 2019; Santana et al., 2012), and canopy and understory foragers to be more abundant in these habitats due to the wider availability of woody plants.

Nest type: Nest type was determined according to Cramp and Simmons (2006) and Storchová et al. (2018) based on five categories: open arboreal nesters, closed arboreal nesters, tree hole/cavity nesters, closed-ground nesters and open-ground nesters. Nest availability is highly dependent on changes in vegetation cover, structure and woody plant density (Parker, 1987). For example, suitable nesting sites for arboreal nesting species are usually less abundant in areas with lower tree density, whereas shrub encroachment may negatively influence ground-nesting species by reducing the availability of open areas for nesting (Sekercioglu, 2006). We would therefore expect ground-nesting species to be less abundant or even absent in shrub-dominated areas, whereas we would expect tree-nesting species to be more abundant in sites with denser woody vegetation.

Habitat guild: We categorized each sampled species as forest species, grassland species or generalists according to habitat requirements based on Cramp and Simmons (2006). This categorization aims to be representative of species' main habitat requirements and their capacity to use multiple habitats. As such, we expect forest associated species to be less abundant in areas with sparse woody vegetation, where the availability of their primary feeding and nesting resources is likely lower (Newbold et al., 2013). In contrast, we expect grassland species to be more abundant in areas with a more open habitat structure (Donald, 2001) and generalist species to be equally ubiquitous across the habitat gradient due to their capacity to explore multiple resources.

Wing aspect ratio: For most species we obtained wing aspect ratio data in published resources but for some species we calculated it as the ratio between squared wing span and wing area (Pennycuick, 2008). All sources used to obtain wing measurements are in S3 Table. Wings with higher aspect ratios provide better energy efficiency during flight, allowing birds to fly longer distances with a lower energetic cost (Mönkkönen, 1995; Rayner, 1988; Fernández and Lank, 2007). Aerial insectivores feeding in open habitats with sparse and shorter vegetation often show higher wing aspect ratios (Rayner, 1988; Warrick, 1998). On the other hand, species foraging in denser vegetation usually show lower wing aspect ratios, associated with shorter and more rounded wings, which allow better manoeuvrability (Vanhooydonck et al., 2009, Moermond and Denslow, 1985). We expect that species with lower values of this trait will be more abundant in areas with higher shrub cover/tree density, where species with higher wing aspect ratios are expected to be less abundant.

Body mass: We used the EltonTraits 1.0 database to collect bird body mass information (Wilman et al., 2014). Body mass is also an indicator of species range size and habitat occupation, with larger species often occupying wider and more open areas (De la Montaña et al., 2006, Galván and Benayas, 2011).

Larger species may thus benefit from non-intensively managed wood-pastures, where a heterogeneous vegetation structure may provide more adequate foraging grounds and higher abundance and variety of food resources (Dehling, 2014).

Table 1

Table provides the description and the type of each bird trait used in the analysis.

Traits	Description	Type
Feeding guild	Diet throughout the breeding season; Granivore Insectivore Omnivore	Categorical
Foraging strata	Percent use of: Canopy Mid high (above 2 m) Understory (below 2 m) Ground	Percentage
Nest type	OA: Open arboreal, cup in bush, tree, on cliff ledge H: Hole, in tree, bank, ground, crevice GC: Ground close, nest in tussock, very close to ground CA: Closed arboreal G: Ground directly	Categorical
Habitat guild	Type of habitat that species mainly occupies: Grassland species Generalists species Forest species	Categorical
Wing aspect ratio (unitless)	Ratio between squared wing span and wing area	Continuous
Body mass (g)	Unsexed body mass value	Continuous

2.4. Environmental data

The habitat structure of each study area was characterized with a set of variables including understory

cover and height, tree density and habitat heterogeneity. These variables were selected as indicators of a management gradient which ranged from areas with regular and active human management (e.g. regular grazing, shrub removal, etc.) towards more sparsely used areas (e.g. occasional grazing, no shrub removal) resembling process of land abandonment. To measure these indicators, herb cover and shrub cover (% of ground cover), herb height (in 5 cm classes up to 25 cm) and shrub height (in 25 cm classes up to 150 cm) were visually estimated by the same observer at each sampling station. After that, shrub and herb height measurements were transformed to numeric values up to 0.25 and 1.50 m, respectively. Tree density (number of trees per hectare) and canopy cover (% ground cover covered by tree crowns) were estimated visually using aerial images available in Google Earth v7.1. Later, we calculated a habitat heterogeneity index using six habitat variables; herb cover, herb height, shrub cover, shrub height, tree density and canopy cover applying the formula of "max. value – min.value/mean value" for each habitat variable and the resulting values were summed to obtain a single heterogeneity value for each wood-pasture (Rotenberry and Wiens, 1980). Finally, we performed Principal Components Analysis (PCA) (Jolliffe, 2002) combining variables of herb and shrub cover, herb and shrub height, tree density and habitat heterogeneity to reduce the number of variables and avoid issues associated with variable collinearity (Dormann et al., 2013). The first and the second axis values of the PCA were used to represent the main habitat management gradients in the subsequent analysis (Table 2). The first PCA axis is mostly representative of ground vegetation habitat structure and ranges from actively managed herb dominated areas to shrub dominated areas, where the management intensity is lower. The second PCA axis represents a gradient from sparsely wooded and heterogeneous areas to densely wooded and homogeneous areas, where shrub cover and height are also lower due to higher management intensity (Fig. 2).

Table 2

PCA representation of the habitat variables used as management indicators. PC1 explains 46% of the variation majorly indicating herb and shrub cover changes throughout the study area. PC2, explaining 20% of the variation in the habitat structure, is mostly correlated to changes in habitat heterogeneity, tree density (number of trees per hectare).

Variables	Correlation of the variables to the PCA dimensions	
	Axis1 (46%)	Axis2 (20%)
Herb cover	-0.5735659	0.1074351
Tree density	0.2954380	0.5221969
Shrub cover	0.5675688	-0.1349756
Herb height	-0.3984235	0.1573461
Shrub height	0.2208402	-0.4852495
Heterogeneity	-0.2325783	-0.6613054

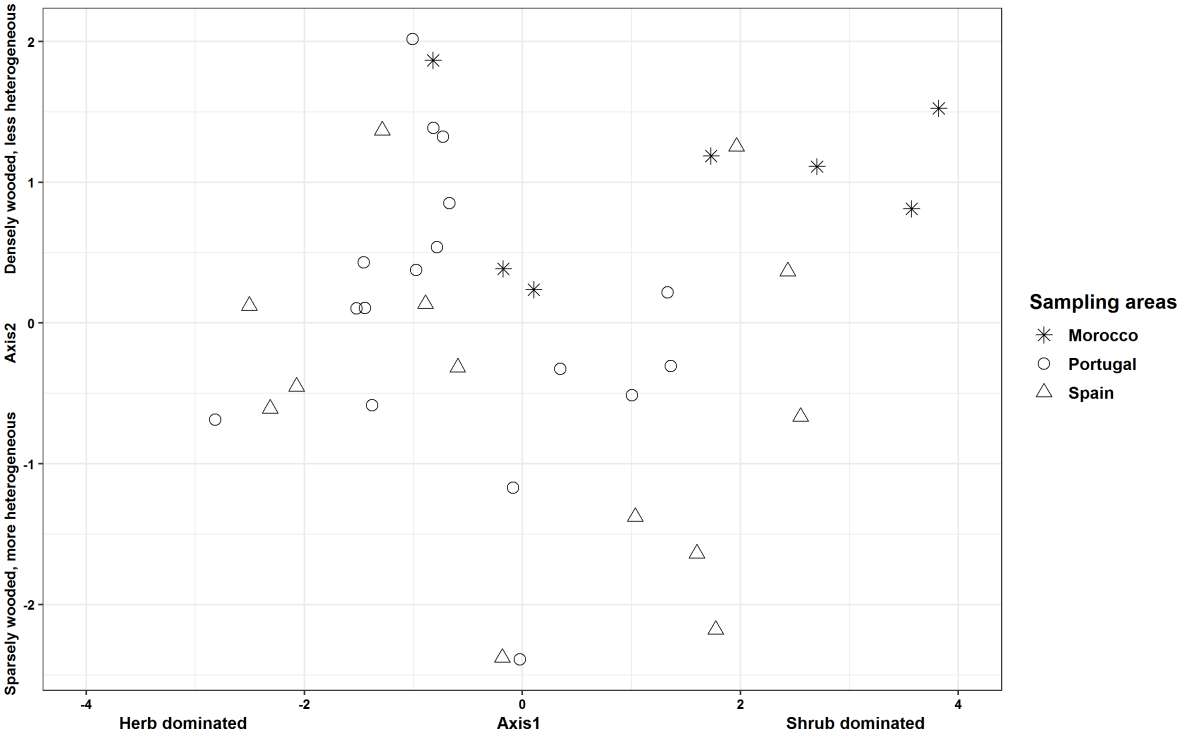

Fig. 2. Figure showing the distribution of sampling points along the habitat structure represented by PCA axes (Axis1-46% and Axis2-20%).

2.5. Data Analysis

We assessed bird taxonomic diversity using species richness (total number of species) and Shannon–Wiener diversity indexes (Shannon and Weaver, 1949). We also assessed bird functional diversity by calculating multi-trait functional richness (FRic), functional dispersion (FDis) and functional evenness (FEve) indices. FRic represents the number of functional groups in the community. Contrary to functional richness, functional dispersion (FDis) and functional evenness (FEve) indices are independent from species richness (Mason et al., 2005; Villéger et al., 2008). Functional dispersion (FDis) measures the degree of dissimilarity in a community by calculating the weighted (by species relative abundances) mean distance of each species to the weighted centroid of all species in multidimensional trait space of the community. Functional evenness (FEve) measures the evenness of traits weighted by species abundances distribution in the community trait space. Thereby these three indices reflect how and to what extent trait diversity varies in relation habitat characteristics (Villéger et al., 2008; Laliberté and Legendre, 2010). Before each index was calculated, we assessed the correlation between traits using Spearman correlations because highly correlated traits may bias measurements of functional diversity (Lepš et al., 2006). There were no significant correlations (p>0.05), therefore we included all traits in the analysis of multi-trait functional diversity indices, giving each trait an equal weight.

We also calculated the community weighted means (CWM) index of each trait to test how individual trait composition responded to changes in habitat structure. For continuous traits, CWM values represent the mean value of that trait in the community, whereas for categorical and binary traits they correspond to the proportion of each category in the community, thus representing their relative abundance (Lavorel et al., 2008).

All analyses were performed in R. 3.5.2 computing environment (R Core Team, 2019). Species richness and Shannon index were calculated using "specnumber" and "diversity" functions respectively, in the "vegan" package (Oksanen et al., 2016). Functional diversity and functional composition indices were calculated using the 'dbFD' function in package 'FD' (Laliberté et al., 2014). Finally, we tested the relationship between species diversity and functional trait variables in relation to the habitat structure gradients represented by PCA axes using generalized linear models implemented with the "glm" function in "stats". Adjusted R-squared values were calculated for each model using "rsq" function in "rsq" package (Zhang, 2018). All figures were produced using "ggplot2" (Wickham et al., 2016).

3. Results

3.1. Species richness and Shannon diversity

There were no evident changes in species richness or Shannon diversity in relation to the first axis, which represents habitat structure (Figs. 3a and 3b; Table 3). On the other hand, both species richness and diversity decreased towards more densely wooded and less heterogeneous areas (represented by higher values on axis 2), although the observed trends were not statistically significant (Figs. 3c and 3d; Table 3).

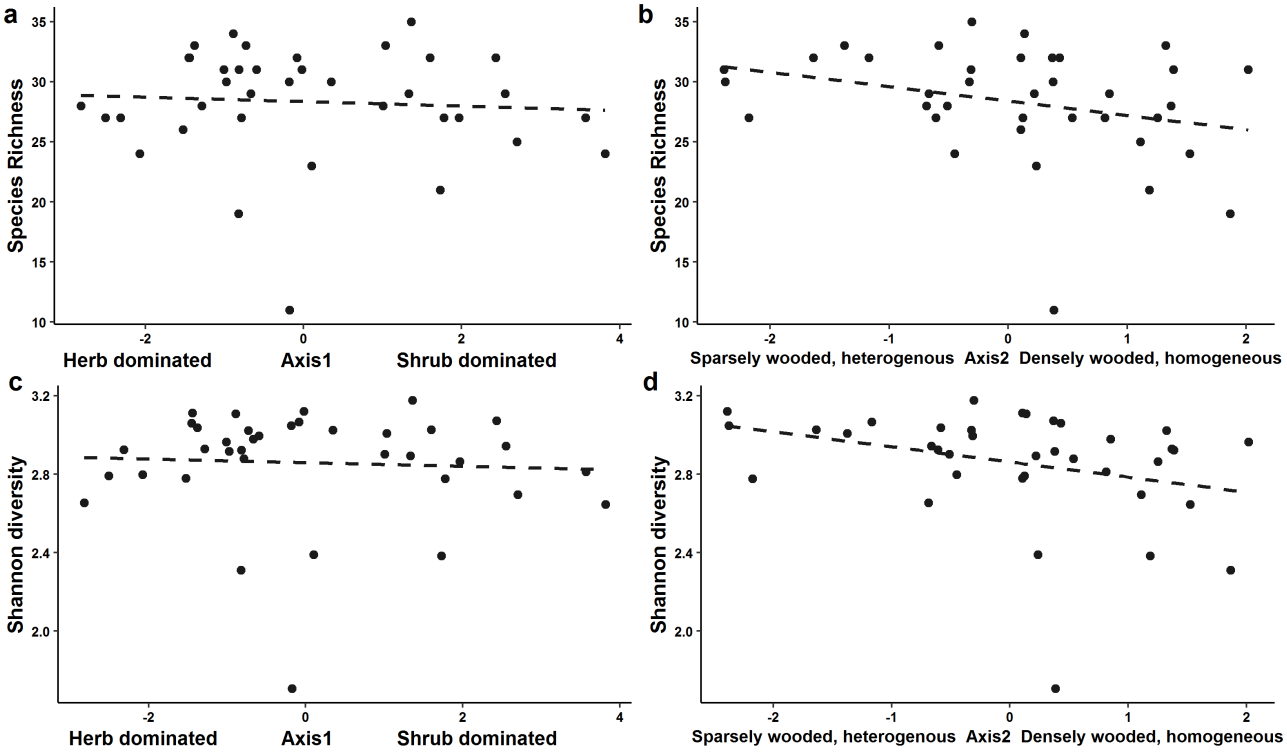

Fig. 3 Relation of bird species richness and Shannon diversity to habitat structure represented by PCA dimensions. Differences in species richness (a) and diversity (c) across PCA axis 1 are not significant. Both species richness (b) and diversity of birds (d) decrease along PCA axis 2 but the differences are only nearly significant. Dashed lines indicate the non-significant (p>0.05) generalized linear model results. See Table 3 for test statistics of linear models.

Table 3

Generalized linear model results show the relation of species richness and Shannon diversity index to the habitat structure which are represented by the first and the second PCA dimensions. The values in the table represent estimate, standard error (SE), significance level (p≤0.05) and adjusted correlation (R-squared) values resulted from the models.

Taxonomic diversity	PCA Axis 1 (46%)				PCA Axis 2 (20%)			
	Estimate	SE	*p*	R^2	Estimate	SE	*p*	R^2
Intercept	28.338	0.776	<0.001	-0.023	28.393	0.744	<0.001	-0.05
Species richness	-0.186	0.459	0.69		-1.197	0.663	0.08	
Intercept	2.858	0.047	<0.001	-0.025	2.862	0.044	<0.001	-0.069
Shannon diversity	-0.009	0.027	0.74		-0.077	0.040	0.06	

3.2. Functional diversity

Despite the lack of statistically significant changes in species richness and Shannon diversity in relation to habitat structure, functional diversity responded significantly to this factor, generally decreasing towards areas with a lower intensity of management. Functional richness (FRic) showed a nearly-significant decrease in relation to PCA axis 1, and thus towards areas with less human intervention, where shrub cover and shrub height are higher (Table 4). Functional dispersion (FDis) and functional evenness (FEve) also decreased towards shrub-dominated and less heterogeneous areas (Fig. 4), and in both cases the decrease was statistically significant (Table 4). No significant associations were detected between any of the FD indices calculated and the second PCA axis (Table 4).

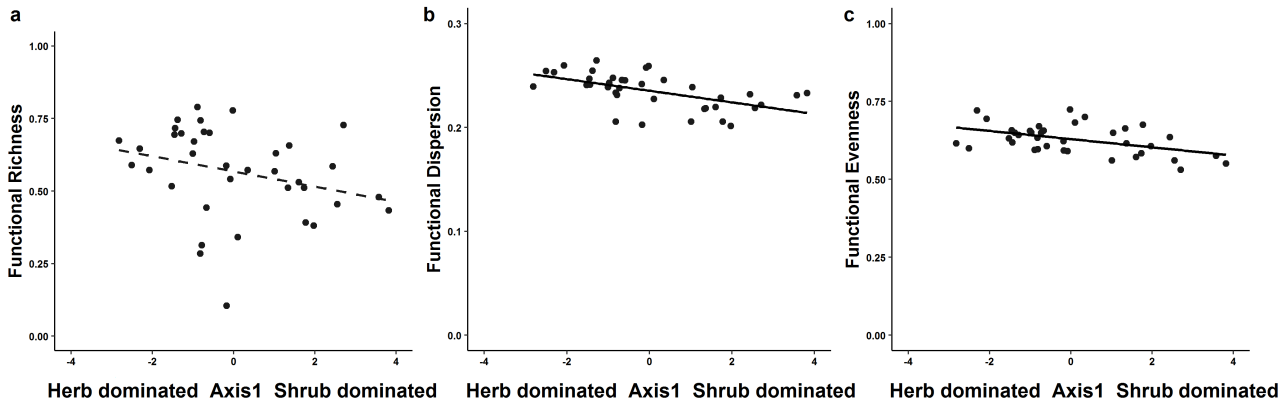

Fig. 4 Relation of bird functional diversity to habitat structure represented by the first PCA axis. All variables show a decrease towards shrub dominated, less managed areas and this relationship is not statistically significant for functional richness (a), however it was significant for bird functional dispersion (b) and functional evenness (c). Solid lines indicate the significant ($p \leq 0.05$) and the dashed line indicates the non-significant linear model results. See Table 4 for test statistics of linear models.

Table 4

Generalized linear model results show the relation of functional diversity (FD) indices to the habitat structure which are represented by the first and the second PCA dimensions. The values in the table represent estimate, standard error (SE), significance level ($p \leq 0.05$) and adjusted correlation (R-squared) values resulted from the linear models.

Functional diversity	**PCA Axis 1 (46%)**				**PCA Axis 2 (20%)**			
	Estimate	**SE**	***p***	**R^2**	**Estimate**	**SE**	***p***	**R^2**
Intercept	0.567	0.024	<0.001	-0.057	0.567	0.025	<0.001	-0.006
Functional richness (FRic)	-0.026	0.014	0.08		-0.019	0.022	0.39	
Intercept	0.235	0.002	<0.001	-0.288	0.235	0.003	<0.001	-0.011
Functional dissimilarity (FDis)	-0.005	0.001	**<0.001**		-0.001	0.002	0.45	
Intercept	0.629	0.007	<0.001	-0.206	0.628	0.007	<0.001	-0.025
Functional evenness (FEve)	-0.01	0.004	**≤0.01**		-0.009	0.006	0.17	

3.3. Functional composition

We observed significant variations in feeding guild, foraging strata, nest type and habitat use traits of birds along the management gradient represented by the first PCA axis (Table 5). CWM of grassland species and generalists significantly decrease towards shrub dominated areas, while forest species show the opposite trend. However, it should be noted that forest species are still well represented in more open and heterogeneous areas, where they compose approximately half of the observed bird communities, whereas grassland specialist species are often absent in shrub dominated areas (Fig. 5a; Table 5).

CWM of granivores decreases significantly towards shrub-dominated areas. However, the CWM of omnivore and insectivore species did not vary significantly in relation to any of the habitat variables, indicating their relative abundance remains more constant independently of habitat structure (Fig. 5b; Table 5). The relative abundance of ground-foragers also decreases with higher shrub cover in areas tending towards abandonment, while species foraging in the canopy and lower vegetation strata benefit from the abundant woody vegetation available in these areas (Fig. 5c; Table 5). Closed-ground nesters are better represented in open and heterogeneous areas maintained by more active human management. On the other hand, arboreal nesting birds are more prevalent in less managed areas with higher shrub cover and tree density (Fig. 5d; Table 5)

Wing aspect ratio of birds decreases from sparsely wooded and more heterogeneous areas to less heterogeneous areas with dense woody vegetation, as suggested by the significant negative relationship between this trait and the second PCA axis (Fig. 6; Table 5). Similarly, we did not observe significant variations in body mass across the study area. Tree/cavity and bare ground nesting types were poorly represented in our samples and we did not detect any significant differences in their relative abundance in relation to habitat variables (Table 5).

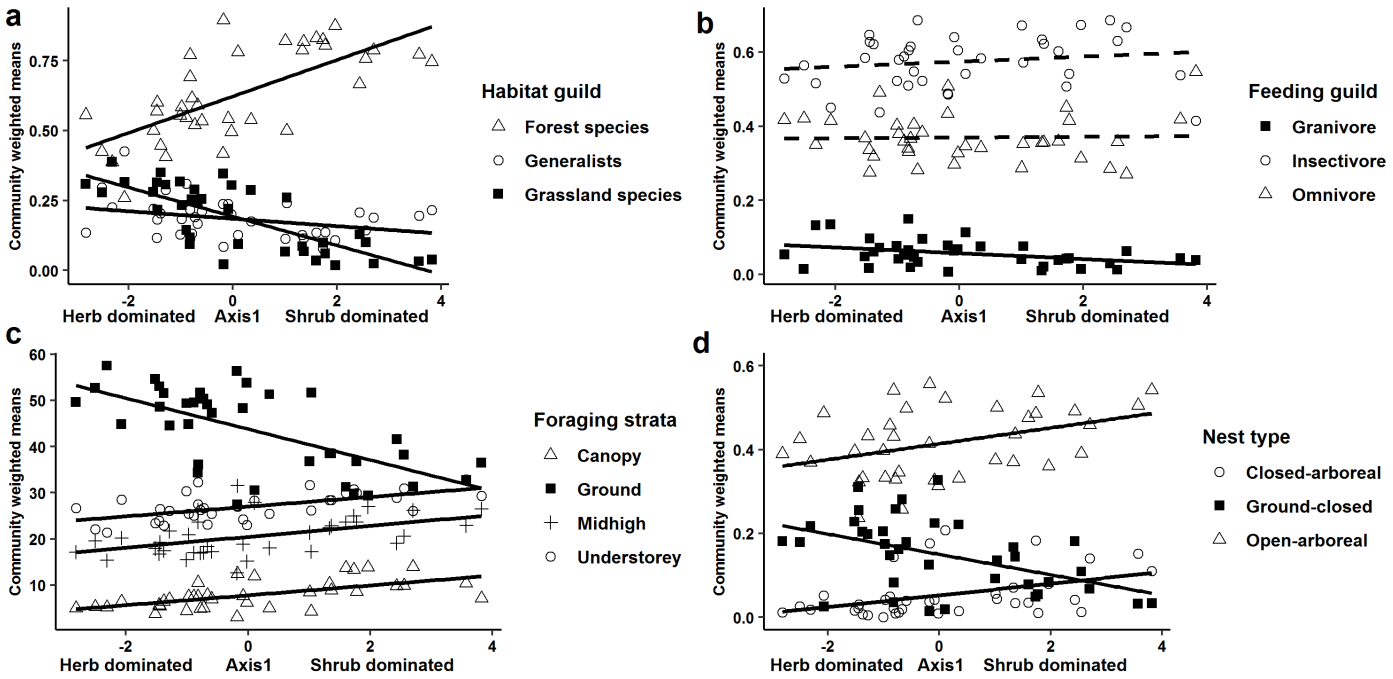

Fig. 5. Community weighted means (CWM) of habitat guild (a), feeding guild (b), foraging strata (c) and nest type (d) across management gradient. Relative abundance of granivores, closed-ground nesters, ground-foragers, generalists and grassland species substantially decreases towards to shrub dominated, less managed areas. Arboreal nesters, canopy and understory foragers and forest species highly benefit from shrublands. Solid lines indicate the significant ($p \leq 0.05$) and the dashed lines indicate the non-significant linear model results. See Table 5 for test statistics of linear models.

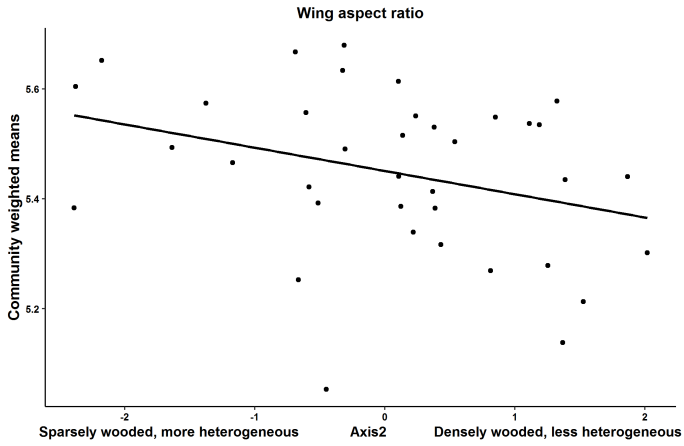

Fig. 6. Relation of community weighted means (CWM) of wing aspect ratio across habitat structure. Prevalence of species with a higher wing aspect ratio decreases significantly towards less heterogeneous areas with higher tree density as represented by second PCA axis (%20). See Table 5 for details on test statistics.

Table 5

Generalized linear model results show the relation of community weighted means (CWM) values of traits to the habitat structure represented by the first and the second PCA dimensions. Table represent the estimate, standard error (SE), significance level ($p \leq 0.05$) and adjusted correlation (R-squared) values of the models.

Traits	**PCA Axis 1 (46%)**				**PCA Axis 2 (20%)**			
	Estimate	**SE**	***p***	**R^2**	**Estimate**	**SE**	***p***	**R^2**
Habitat guild								
Intercept	0.192	0.012	<0.001		0.190	0.019	<0.001	
Grassland species	-0.051	0.007	**<0.001**	-0.56	-0.022	0.017	0.19	-0.020
Intercept	0.184	0.0112	<0.001		0.184	0.0117	<0.001	
Generalists	-0.014	0.007	**≤0.05**	-0.078	-0.010	0.012	0.37	-0.008
Intercept	0.622	0.019	<0.001		0.625	0.026	<0.001	
Forest species	0.065	0.01	**<0.001**	0.46	0.031	0.023	0.19	0.021
Feeding guild								
Intercept	0.0571	0.0055	<0.001		0.0566	0.0059	<0.001	
Granivores	-0.007	0.003	**≤0.05**	-0.113	-0.001	0.005	0.79	-0.026
Intercept	0.369	0.010	<0.001		0.368	0.0106	<0.001	
Omnivores	-0.001	0.006	0.87	-0.027	-0.007	-0.009	0.45	-0.011
Intercept	0.573	0.011	<0.001		0.574	0.0117	<0.001	
Insectivores	-0.006	0.006	0.33	-0.0005	-0.005	-0.010	0.58	-0.019

Traits	PCA Axis 1 (46%)				PCA Axis 2 (20%)			
	Estimate	**SE**	***p***	**R^2**	**Estimate**	**SE**	***p***	**R^2**
Foraging strata								
Intercept	2.740	0.072	<0.001		2.74	0.087	<0.001	
Canopy	0.186	0.042	**<0.001**	0.34	0.111	0.077	0.16	0.024
Intercept	20.46	0.621	<0.001		20.46	0.653	<0.001	
Midhigh	1.182	0.367	**≤0.01**	0.20	1.432	0.582	0.08	0.12
Intercept	26.99	0.389	<0.001		27.04	0.480	<0.001	
Understory	1.051	0.230	**<0.001**	0.35	0.551	0.428	0.21	0.017
Intercept	43.78	1.143	<0.001		0.0229	0.0007	<0.001	
Ground	-3.345	0.677	**<0.001**	-0.39	-2.508	1.260	0.07	-0.076
Nest type								
Intercept	0.201	0.016	<0.001		0.202	0.018	<0.001	
Closed arboreal	0.029	0.009	**≤0.01**	0.15	0.025	0.016	0.11	0.085
Intercept	0.150	0.0126	<0.001		0.149	0.014	<0.001	
Ground close	-0.024	0.007	**≤0.05**	-0.21	-0.012	0.012	0.32	-0.0004
Intercept	0.413	0.0128	<0.001		0.415	0.0139	<0.001	
Open arboreal	0.018	0.007	**≤0.05**	0.12	-0.005	-0.012	0.67	-0.023
Intercept	0.365	0.0115	<0.001		0.3652	0.0116	<0.001	
Tree hole, cavity	-0.006	0.006	0.38	-0.006	-0.004	-0.010	0.64	-0.022
Intercept	0.0178	0.0027	<0.001		0.0179	0.0027	<0.001	
Ground	-0.002	0.001	0.12	-0.041	-0.004	0.002	0.08	-0.056
Intercept	5.449	0.024	<0.001		5.450	0.0236	<0.001	
Wing aspect ratio	-0.01	0.014	0.36	-0.004	-0.042	0.021	**≤0.05**	-0.08
Intercept	46.509	1.774	<0.001		46.51	1.775	<0.001	
Body mass	-0.1	1.050	0.92	-0.028	0.090	1.583	0.95	0.028

4. Discussion

4.1. Habitat changes associated with land abandonment lead to changes in bird functional diversity but not in taxonomic diversity

Our results show that changes in the vegetation structure and habitat heterogeneity of wood-pastures associated with land abandonment processes did not result in significant taxonomic diversity changes but substantially influenced trait-level diversity of birds during the breeding season. Both species richness and Shannon diversity metrics did not vary significantly in response to changes in habitat structure, suggesting that both actively managed and the less even wood-pastures with habitat features emerging from land abandonment processes are still represented with diverse species assemblages (Fig. 3; Table 3). However, our results also indicate that changes in habitat structure resulting from land abandonment lead to slight declines in the number of bird functional groups (FRic) from actively managed areas to less managed areas. In addition, both functional dispersion (FDis) and functional evenness (FEve), representing the level of trait dissimilarity and trait evenness, decrease significantly in less managed areas (Fig. 4; Table 4). This suggests that trait assemblages in wood-pastures with less human intervention may be dominated by less dissimilar traits than those areas undergoing active human management. Moreover, lower functional evenness towards less managed areas may show the reduced efficiency in resource use for birds (Hillebrand et al., 2008; Crowder et al., 2010). Several studies report contrasting trends in species and trait-level responses to different land- uses and management strategies, suggesting the need to explore different dimensions of biodiversity to understand the complex relation of species to the ecosystem (Carmona et al., 2012; Devictor et al., 2010). We concur with this view, as our results indicate more pronounced trait-level responses to changes in habitat structure than those observed at the species level. These results indicate variations in niche structure resulting from different management strategies, which can benefit or impair species

with specific traits without leading to changes in the overall number of species present in the habitat (Gagic et al., 2015). Ultimately, an in-depth assessment of changes in biodiversity and ecosystem dynamics associated with different land use practices requires more than the simple analysis of taxonomic changes and should also take into consideration the changes in traits related to specific ecological functions. Our findings reveal that lower functional dispersion of less managed areas is majorly due to the loss of traits associated to grassland birds (Fig. 5; Table 5). Indeed, our analysis of the relative abundance of individual traits (CWM) in relation to habitat structure suggests that specific traits may be particularly susceptible to changes in habitat resulting from land abandonment.

Land abandonment in wood-pastures is often characterised by a reduction in grazing intensity and the absence of other management activities commonly used to improve grazing efficiency, such as shrub removal, resulting in higher tree and shrub densities, denser canopies and a general loss of habitat heterogeneity (Castro and Freitas, 2009; Oldén et al., 2017; Peco et al., 2006). Grassland species usually depend on open mosaics of habitats to feed and nest (Batary et al., 2007a; Reino et al., 2010), so the presence of denser and taller woody vegetation is likely to reduce the availability of suitable conditions for these species (Preiss et al., 1997; Sirami et al., 2007; Spitzer et al., 2008; Sebek et al., 2015). Our results suggest that this is indeed the case in wood-pastures as the relative abundance of grassland species decreased towards areas with denser and taller shrubby vegetation. Grassland bird populations have suffered severe declines in recent decades all across Europe and such declines have often been associated with land-use intensification (Donald et al., 2006; Butler et al., 2010), but our findings underline that land abandonment is likely to be another factor negatively affecting this guild. More generally, other traits associated with the exploitation of resources that are often only available in open areas, such as ground nesting, ground feeding and granivory, also decreased towards abandoned

areas. These changes are likely due to the presence of dense shrubby vegetation in these areas, which can substantially restrict seed availability, predator detectability and the presence of suitable ground foraging sites for these species (Santana et al., 2012; Leal et al., 2019).

In contrast, our results suggest that forest species benefit from habitat changes associated with land abandonment (Fig. 5; Table 5) and similar results have been observed in wood-pastures across Europe (Sirami et al., 2009; Nikolov et al., 2011; Jakobsson et al., 2018). Dense shrublands are known to benefit forest species such as Robin (*Erithacus rubecula*), Blackcap (*Sylvia atricapilla*) and Wren (*Troglodytes troglodytes*) by providing feeding resources and reducing predation (Tellería, 2001; Santana et al., 2012). Furthermore, nesting availability will be greater for arboreal nester forest species and such species are likely to benefit from densely wooded areas, as our results suggest (Fig. 5). We also observed significant differences in birds associated with different foraging strata (Fig. 5; Table 5), which can be informative of the way birds use the habitat under different management strategies (Martin and Possingham, 2005). Specifically, the abundance of understory and canopy foragers increases in less managed areas where both shrub and tree densities are higher (Fuller, 2012; Ikin et al., 2012), whereas ground foragers tend to decrease, ultimately suggesting that land abandonment leads to changes in the overall use of different foraging strata. There may be important changes in ecosystem dynamics related to this vertical shift towards birds feeding mostly on higher vegetation layers in less managed areas. For example, many pest species of cork and holm oaks (the main tree species supporting the studied wood-pasture system) spend at least part of their early life-cycle on or under the ground (Ceia and Ramos, 2016). Ground feeding bird species can play an important role in controlling the populations of these pests during their earlier life-stages, but this may not be the case in areas where ground vegetation is too dense for birds to find suitable feeding areas. We also observed that bird assemblages in more homogeneous areas with higher tree density and less shrubs tend to feature more

birds with a lower wing aspect ratio (Fig. 6; Table 5). Lower values of wing aspect ratio are associated with shorter and more rounded wings, which allow for better manoeuvrability in densely wooded habitats (Vanhooydonck et al., 2009) but are less suited for longer distance flights. It may be the case that these birds fly shorter distances and end up having smaller home ranges. In contrast, species with a higher wing aspect ratio tend to move greater distances and require more open habitats (Norberg 1995; Reif et al., 2016).

Ultimately, our results suggest that maintaining higher response trait diversity may be important to ensure the resiliency of wood-pastures under various pressures (Mori et al., 2013; Standish et al., 2014; Plieninger and Bieling, 2013). In addition, we should underline that the traits we analysed are both "response and effect traits", implying that many of the trait-level changes observed may also reflect greater effect on the ecosystem dynamics and the ecosystem services in wood-pastures (de Bello et al., 2010; Plieninger et al., 2014; Torralba et al., 2016). However, it is also clear that a more in-depth assessment of how changes in habitat structure may affect the provision of ecosystem services such as pest predation, seed dispersal and weed control that are provided by birds (Ceia and Ramos, 2016; Whelan et al., 2008; Sekercioglu, 2012) is needed to fully evaluate the consequences of land abandonment on the natural value of wood-pastures.

4.2. Human management is needed to maintain functionally diverse bird communities in wood-pastures

Our results clearly evidence the important role of human management in maintaining bird functional diversity in wood-pastures. Extensive grazing acts to maintain the characteristic spatial heterogeneity of wood-pastures (Isselstein et al., 2005; Almeida et al., 2015), which is crucial to provide diverse feeding and nesting resources for birds (Vickery et al., 2001; Tews et al., 2004; Stein et al., 2014), particularly during the breeding season (Wirtitsch et al., 2001; Mag and Ódor, 2015). Grassland species

are especially dependent on resources that are only available in more open and heterogeneous areas (Fig. 5; Table 5), which are usually sustained by extensive grazing (Benton et al., 2003; Batary et al., 2007a). These resources include suitable feeding areas for more food resources for ground-foragers and lower predation risk for ground-nesting species (Erdõs et al., 2009; Vickery and Arlettaz, 2012; Buckingham and Peach, 2005; Jeliazkov et al., 2016; Leal et al., 2019). Generalist species also seem to be more abundant in areas with active management, whereas forest species benefit from the dense habitat structure that results from land abandonment. However, we should underline that forest species are also present in open managed areas where they comprise approximately half of the bird community, whereas grassland species are often completely absent in densely vegetated areas (Fig. 5). This suggests that by maintaining habitat heterogeneity, actively managed areas can provide a wide range of niches, inclusively for forest species. Forest systems are also undergoing multiple land-use changes, which pose specific challenges for bird species in these habitats (Camprodon and Brotons, 2006; Wade et al., 2013), so maintaining adequately managed wood-pastures may also play an important role in preserving forest bird populations across Europe. This may be particularly important in the context of southern Europe, where many forest birds have the southern limit of their distributions, and where changes in habitat structure as well as climate change are already having a toll in forest bird populations (Correia et al., 2015b).

While human management seems necessary to maintain heterogeneous wood-pasture landscapes, the intensity of human intervention also plays a key role. The impacts of land-use intensification have been widely reported (Newbold et al., 2015; Gossner et al., 2016) and there is evidence that in highly exploited systems, reducing management intensity level can be advantageous providing more suitable and connected habitats for species narrower niche requirements (Eldridge et al., 2011; Queiroz et al., 2014). On the other hand, studies focusing on multiple species responses to land abandonment also

report the potential threats of this change in land-use to the overall biodiversity value of managed habitats (Suarez-Seoane et al., 2002; Horák et al., 2018; Sebek et al., 2015). Specifically, land abandonment may ultimately lead to the functional homogenization of biological communities in Mediterranean habitats (Ehlers Smith et al., 2015, Clavero and Brotons, 2010) due to a loss of habitat heterogeneity, an assessment that our results also support. It is obvious that both habitat intensification and abandonment can have prejudicial consequences for the biodiversity value of wood-pastures, whose preservation depends on the maintenance of spatial habitat heterogeneity that emerges from multi-purpose management strategies (Roellig et al. 2016; Mönkkönen et al. 2014; Götmark 2013). As more traditional management strategies struggle to maintain the economic sustainability of wood-pastures, the challenge for the future is to find simple and inexpensive management strategies that conciliate economic and natural values in wood-pastures.

5. Conclusions

To conclude, our results show that substantial changes in the functional diversity and functional composition of birds occur in response to changes in vegetation structure and habitat heterogeneity, which result from different management strategies in Mediterranean wood-pastures. Wood-pastures with a habitat structure that is characteristic of land abandonment processes are favoured by forest birds that depend on resources provided by woody vegetation, but avoided by grassland as well as generalist species, resulting in the absence of specific life-history traits that ultimately lead to loss of bird functional diversity in these areas.

Wood-pastures are fragile ecosystems, undergoing a transformation process from multi-functional, heterogeneous habitats to homogeneous areas due to reduced management or overuse as a result of multiple socio-economic pressures (Hartel et al., 2015). The abandonment of traditional management

and the subsequent encroachment of woody vegetation is increasingly reported to threaten the biodiversity of multiple habitats (Queiroz et al., 2014). Balancing the biodiversity and economic value of human-modified habitats is one of the main challenges in improving conservation efforts (Lindenmayer et al., 2008; Graves et al., 2007; Landis et al., 2017). Maintaining human management in wood-pastures is essential to preserve their high natural value but will require the development of innovative low-cost and nature-based solutions that are able to conciliate the economic and natural sustainability of wood-pastures across Europe (Doxa et al. 2010; Plieninger et al. 2015).

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Table S1: Bird abundance data.

Sampling areas	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
	Portugal	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Portugal	Spain	Spain	Spain	Morocco	Morocco	Morocco	Morocco	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Morocco	Morocco	Morocco	Portugal	Portugal	Spain	Spain	Portugal	Portugal	Portugal
Alauda arvensis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4	3	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
Alectoris rufa	0	0	0	0	0	1	1	0	0	3	0	0	1	0	0	0	3	1	5	7	2	3	0	3	0	2	0	0	0	0	0	2	1	0	0	1	2
Aegithalos caudatus	3	0	0	1	2	0	0	0	0	2	0	4	2	0	0	0	0	0	0	5	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Burhinus oedicnemus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	2	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Carduelis carduelis	1	2	3	12	4	5	2	10	7	9	1	3	2	0	5	1	0	6	6	6	1	3	11	2	1	3	3	1	1	3	5	4	8	12	6	5	9
Linaria cannabina/Carduelis cannabina	0	0	1	2	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Certhia brachydactyla	16	9	19	18	18	11	20	3	4	16	15	16	14	0	1	0	1	14	6	13	10	13	14	14	15	18	15	14	2	4	23	19	13	18	18	18	5
Cisticola juncidis	0	0	0	0	0	0	0	2	10	8	0	0	0	0	0	0	0	0	9	0	14	0	0	0	1	2	2	0	2	1	2	2	0	0	0	0	10
Cuculus canorus	2	9	4	4	0	5	0	6	1	3	0	2	2	0	0	0	0	0	0	2	3	3	4	2	3	3	2	1	1	0	0	4	3	4	6	3	3	0
Coturnix coturnix	0	0	1	1	0	0	0	2	4	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	3	1	3	0	3	0	1	2	0	0	0	1	0
Chloris chloris/Carduelis chloris	1	3	3	5	3	8	0	7	9	8	0	0	3	0	6	27	2	1	3	0	0	4	3	1	1	3	1	0	1	0	7	8	12	6	3	7	4
Columba palumbus	2	6	12	1	5	0	7	1	3	1	7	0	5	5	1	1	1	0	4	6	0	0	1	0	0	0	0	2	14	8	4	1	1	0	3	0	0
Cyanopica cyanus/Cyana cyanus	0	0	3	0	0	3	22	22	19	0	0	0	0	0	0	0	0	0	2	5	0	5	1	0	0	14	0	0	0	0	0	0	0	0	0	0	0
Corvus corone	0	2	7	0	0	0	2	0	1	0	0	1	0	0	0	1	1	0	0	0	3	0	2	2	2	1	0	1	0	0	1	5	0	0	1	0	1
Dendrocopos major	3	3	2	1	4	5	2	0	2	4	7	6	4	20	13	23	12	3	10	6	6	3	8	6	4	8	4	5	3	11	2	4	5	0	2	2	8
Erithacus rubecula	10	0	0	0	2	0	0	0	0	0	17	8	10	0	0	0	0	9	0	0	0	0	0	0	0	0	0	2	25	20	0	0	0	0	0	0	0
Emberiza cirlus	2	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	2	1	3	0	2	0	2	2	0	0	0	0	0	0	2	1	1
Fringilla coelebs	21	38	46	42	46	39	46	6	23	19	32	37	27	62	41	47	41	26	19	23	28	41	41	22	37	26	35	33	24	20	45	59	42	38	36	20	49
Galerida cristata	0	0	0	2	0	7	5	0	4	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	0	5	0	0	0	0	0	0	1	18	6	7	0
Garrulus glandarius	3	1	0	1	1	0	0	0	0	4	5	4	3	0	0	0	0	0	2	5	2	0	2	5	1	6	0	3	4	5	0	1	3	2	1	3	1
Hippolais polyglotta	1	0	1	1	0	0	0	0	1	2	0	1	0	0	0	0	0	1	2	0	3	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2	
Jynx torquilla	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	
Luscinia megarhynchos	16	14	5	1	4	7	0	0	3	15	2	0	5	0	0	0	0	8	12	6	6	0	6	6	6	3	8	0	1	2	3	1	3	6	8	5	8
Lullula arborea	6	12	24	19	4	18	25	1	6	15	2	4	0	0	2	5	1	6	17	26	15	15	3	22	8	24	17	1	0	1	23	15	14	16	7	17	6
Lanius senator	0	11	9	15	1	11	14	20	2	0	0	0	0	0	1	0	0	0	0	1	1	4	0	2	1	12	1	0	0	0	10	1	9	14	13	5	0
Muscicapa striata	0	0	0	4	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3	0	0	0
Emberiza calandra/Miliaria calandra	1	0	0	12	0	34	24	2	25	24	4	0	0	0	0	0	0	0	29	19	25	23	0	25	5	28	17	0	1	1	29	28	25	15	21	17	11
Oenanthe oenanthe	0	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oriolus oriolus	6	2	3	3	3	2	1	0	3	0	0	0	6	0	1	0	0	6	6	3	1	5	0	5	0	7	0	8	1	1	0	6	14	5	3	0	0
Cyanistes teneriffae/Parus teneriffae	0	0	0	0	0	0	0	0	0	0	0	0	0	25	33	28	26	0	0	0	0	0	0	0	0	0	0	28	19	28	0	0	0	0	0	0	0
Cyanistes caeruleus/Parus caeruleus	13	17	18	15	13	22	19	9	16	25	19	20	21	0	0	0	0	23	14	26	19	24	23	13	23	21	19	0	0	0	18	19	15	11	23	18	10
Parus major	10	6	12	12	11	10	8	15	20	12	21	20	11	15	17	15	8	9	8	11	10	15	7	9	8	10	6	26	17	12	9	7	10	7	11	8	7
Phylloscopus bonelli	8	15	11	0	2	0	0	0	0	0	11	14	13	0	0	1	6	0	0	0	1	1	5	0	9	0	2	10	2	1	0	1	2	0	1	0	2
Phoenicurus phoenicurus	2	7	8	0	4	0	1	0	0	7	0	0	0	0	1	0	2	2	0	4	9	1	16	16	8	5	6	0	0	0	0	0	0	0	1	0	0
Phylloscopus ibericus	1	0	0	0	0	0	0	4	0	3	2	9	3	0	0	0	0	11	0	2	2	4	2	1	11	0	1	0	1	0	0	0	0	0	0	0	0
Petronia petronia	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	16	1	11
Passer hispaniolensis	0	1	10	6	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	5	0	0	0	
Passer domesticus	0	0	6	1	0	9	0	34	14	2	0	2	0	0	0	0	3	2	4	0	3	9	3	0	2	3	0	1	0	0	1	2	1	21	6	0	3
Lophophanes cristatus/Parus cristatus	3	1	0	0	7	2	2	0	0	0	3	3	11	0	0	0	0	1	0	1	0	0	1	9	0	1	0	0	0	4	1	0	0	0	0	3	3
Regulus ignicapilla	2	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Streptopelia decaocto	0	1	8	0	1	7	1	5	0	2	0	0	0	1	5	1	1	0	1	1	1	0	0	1	0	4	0	11	5	5	0	0	3	5	2	1	2
Sturnus unicolor	5	10	16	14	6	21	20	11	14	4	9	1	2	0	1	7	7	1	8	12	14	13	10	13	2	35	15	0	0	0	14	37	15	25	16	12	30
Serinus serinus	18	3	12	9	13	1	1	4	2	9	4	4	6	5	12	17	10	4	3	3	3	6	15	0	4	3	16	6	1	4	6	10	9	17	1	3	10
Sitta europaea	9	11	6	1	6	6	13	0	1	19	9	15	5	0	2	0	0	4	6	9	13	19	19	6	7	12	11	18	0	1	12	12	6	4	15	8	9
Sylvia melanocephala	11	18	4	13	8	0	1	9	13	9	14	5	21	0	1	0	8	10	7	8	7	5	7	5	14	2	5	6	13	16	5	0	8	10	9	14	12
Saxicola rubicola/Saxicola torquatus	1	3	1	2	0	0	0	0	0	2	6	0	0	2	1	1	0	4	5	2	9	2	2	6	2	0	7	1	0	0	0	0	1	0	2	4	13
Sylvia atricapilla	16	0	0	0	1	0	0	0	1	1	0	6	11	0	0	0	0	5	1	0	0	0	1	0	0	0	0	0	14	3	0	0	0	0	0	1	1
Sylvia cantillans	4	6	1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Sylvia undata	0	7	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	5	0	0	1	0	0	0	0
Streptopelia turtur	3	1	0	0	0	15	0	2	0	3	2	0	2	0	2	0	0	0	0	0	0	0	1	0	0	5	0	1	0	0	0	0	0	0	0	0	2
Troglodytes troglodytes	17	1	0	0	2	0	0	0	0	8	15	11	15	0	0	0	0	23	11	3	9	1	6	3	5	2	3	3	7	4	0	0	0	0	1	4	10
Turdus merula	14	13	9	14	10	8	14	6	12	16	22	13	20	2	3	3	1	11	11	14	5	6	13	6	11	6	7	15	19	18	13	3	12	8	7	6	6
Turdus viscivorus	2	5	8	3	2	1	5	0	0	0	3	2	1	4	3	5	2	2	0	1	0	1	0	2	0	1	2	8	0	4	3	3	0	1	1	0	0
Upupa epops	3	4	9	5	0	11	9	10	2	1	0	0	0	0	0	7	0	1	0	0	0	6	0	0	0	5	4	0	0	0	8	3	4	16	6	3	1

Table S2: Bird trait data.

Species	Feeding guild	Foraging strata-Ground	Foraging strata-Understory (below 2m)	Foraging strata-Mid high (above 2m)	Foraging strata-Canopy	Nest type	Habitat guild	Wing aspect ratio	Body mass
Alauda arvensis	omnivore	100	0	0	0	G	grassland	4.67	37.31
Alectoris rufa	granivore	100	0	0	0	G	grassland	8.07	527.86
Aegithalos caudatus	insectivore	10	40	10	40	CA	forest	4.94	8.6
Burhinus oedicnemus	insectivore	80	20	0	0	G	grassland	7.36	459
Carduelis carduelis	granivore	20	60	20	0	OA	grassland	5.34	16
Linaria cannabina/Carduelis cannabina	granivore	60	20	20	0	OA	grassland	5.93	19.53
Certhia brachydactyla	insectivore	40	30	30	0	H	forest	7.22	8.2
Cisticola juncidis	insectivore	100	0	0	0	GC	grassland	2.7	6.81
Cuculus canorus	insectivore	20	20	40	20	CA	generalist	6.5	111.36
Coturnix coturnix	omnivore	100	0	0	0	G	grassland	5.61	96.28
Chloris chloris/Carduelis chloris	granivore	40	30	30	0	OA	generalist	6.03	26
Columba palumbus	omnivore	80	20	0	0	OA	generalist	5.81	490
Cyanopica cyanus/Cyana cyanus	omnivore	0	20	60	20	OA	generalist	3	95.91
Corvus corone	omnivore	90	0	0	0	OA	forest	5.37	499
Dendrocopos major	insectivore	0	20	40	30	H	forest	4.02	74.94
Erithacus rubecula	omnivore	50	50	0	0	H	forest	4.37	17.7
Emberiza cirlus	omnivore	100	0	0	0	GC	grassland	5.54	25.6
Fringilla coelebs	omnivore	40	30	30	0	OA	forest	5.66	23.81
Galerida cristata	omnivore	100	0	0	0	G	grassland	5.69	42.68
Garrulus glandarius	omnivore	60	20	20	0	OA	forest	4.57	159.46
Hippolais polyglotta	insectivore	0	40	20	40	OA	forest	6.89	11
Jynx torquilla	insectivore	60	20	20	0	H	forest	4.51	34.96
Luscinia megarhynchos	insectivore	70	30	0	0	GC	forest	5.17	19.6
Lullula arborea	insectivore	100	0	0	0	GC	generalist	4.95	26.9
Lanius senator	insectivore	100	0	0	0	OA	grassland	5.63	35.97
Muscicapa striata	insectivore	60	40	0	0	OA	forest	5.23	15.9
Emberiza calandra/Miliaria calandra	omnivore	90	10	0	0	GC	grassland	6.01	48.5
Oenanthe oenanthe	insectivore	100	0	0	0	H	generalist	5.36	25.39
Oriolus oriolus	insectivore	0	0	0	50	OA	forest	7.55	79
Cyanistes teneriffae/Parus teneriffae	insectivore	0	33	33	33	CA	forest	6.02	11.67
Cyanistes caeruleus/Parus caeruleus	insectivore	10	30	30	30	H	forest	6.02	13.3
Parus major	insectivore	0	20	60	20	H	forest	4.57	16.25
Phylloscopus bonelli	insectivore	0	20	0	80	GC	forest	4.63	8.69
Phoenicurus phoenicurus	insectivore	20	40	40	0	H	forest	4.78	14.59
Phylloscopus ibericus	insectivore	25	25	25	25	CA	forest	2.8	8.3
Petronia petronia	omnivore	60	40	0	0	H	generalist	4.84	30.2
Passer hispaniolensis	omnivore	50	50	0	0	CA	generalist	5.83	24.2
Passer domesticus	omnivore	50	50	0	0	H	generalist	5.14	26.51
Lophophanes cristatus/Parus cristatus	insectivore	10	10	20	60	H	forest	6.7	11.04
Regulus ignicapilla	insectivore	0	50	50	0	CA	forest	4.21	5.6
Streptopelia decaocto	granivore	80	10	10	0	OA	generalist	6.03	148.96
Sturnus unicolor	insectivore	50	50	0	0	H	grassland	5	83.66
Serinus serinus	omnivore	60	40	0	0	OA	forest	6.08	11.2
Sitta europaea	insectivore	33	33	33	0	H	forest	5.49	20.37
Sylvia melanocephala	omnivore	20	60	20	0	OA	forest	5.45	11.7
Saxicola rubicola/Saxicola torquatus	insectivore	100	0	0	0	GC	grassland	4.88	14.09
Sylvia atricapilla	omnivore	0	0	100	0	OA	forest	5.94	16.7
Sylvia cantillans	insectivore	10	20	60	10	OA	forest	4.81	9.6
Sylvia undata	insectivore	0	100	0	0	OA	forest	4.81	10.8
Streptopelia turtur	granivore	100	0	0	0	OA	grassland	5.64	132
Troglodytes troglodytes	insectivore	50	50	0	0	H	forest	5.26	9
Turdus merula	insectivore	60	20	20	0	OA	generalist	4.42	102.73
Turdus viscivorus	insectivore	60	20	10	10	OA	generalist	5.59	117.37
Upupa epops	insectivore	100	0	0	0	H	grassland	5.01	66.93

Table S3: All references used to obtain/calculate wing measurements.

Species	References
Alauda arvensis	[1]
Aegithalos caudatus	[1]
Burhinus oedicnemus	[2]
Carduelis carduelis	[1]
Linaria cannabina/Carduelis cannabina	[1]
Cuculus canorus	[1]
Chloris chloris/Carduelis chloris	[1]
Dendrocopos major	[1]
Erithacus rubecula	[1]
Fringilla coelebs	[1]
Garrulus glandarius	[1]
Hippolais polyglotta	[3], [9], [10]
Jynx torquilla	[1]
Luscinia megarhynchos	[1]
Muscicapa striata	[1]
Cyanistes teneriffae/Parus teneriffae	[1]
Cyanistes caeruleus/Parus caeruleus	[1]
Parus major	[1]
Phoenicurus phoenicurus	[1]
Phylloscopus ibericus	[1] (Phylloscopus collybita)
Passer hispaniolensis	[1]
Passer domesticus	[1]
Regulus ignicapilla	[1]
Streptopelia decaocto	[1]
Sturnus unicolor	[2]
Sitta europaea	[1]
Saxicola rubicola/Saxicola torquatus	[1]
Sylvia atricapilla	[1]
Streptopelia turtur	[1]
Troglodytes troglodytes	[1]
Turdus merula	[1]
Turdus viscivorus	[1]
Upupa epops	[1]
Alectoris rufa	[4], [9], [10]
Certhia brachydactyla	[5], [9], [10]
Cisticola juncidis	[6], [9], [10] (Cisticola)
Columba palumbus	[5], [9], [10]
Cyanopica cyanus/Cyan cyanus	[1], [9], [10] (Pica pica)
Lanius senator	[7], [9], [10]
Emberiza calandra/Miliaria calandra	[7], [9], [10]
Coturnix coturnix	[5], [9], [10]
Corvus corone	[5], [9], [10]
Lullula arborea	[5], [9], [10]
Oenanthe oenanthe	[5], [9], [10]
Oriolus oriolus	[8], [9], [10]
Phylloscopus bonelli	[7], [9], [10]
Lophophanes cristatus/Parus cristatus	[5], [9], [10]
Serinus serinus	[3], [9], [10]
Sylvia melanocephala	[7], [9], [10]
Sylvia undata	[7], [9], [10]
Sylvia cantillans	[7], [9], [10] (Sylvia undata)
Petronia petronia	[8], [9], [10]
Galerida cristata	[8], [9], [10]
Emberiza cirlus	[8], [9], [10]

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CHAPTER 5

Wood-pasture abandonment leads to a reduction of insectivore bird functional diversity with potential consequences for pest control

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Abstract

Functional diversity approaches based on effect traits are essential to reveal how land-use changes may affect the biodiversity mechanisms that mediate the provision of ecosystem functions and services. This may be particularly needed for wood-pastures which are under pressure of either intensification or land abandonment influencing taxonomic and functional diversity of several species and potentially leading to changes in ecosystem services although these further impacts are still poorly explored. In this study, we explored the taxonomic and functional diversity of breeding insectivore birds, which play an important role in natural pest control, across a management gradient throughout Iberian Peninsula and North Africa wood-pastures. The habitat structure gradient ranges from actively managed areas with heterogeneous vegetation structure, towards less heterogeneous and shrub-dominated areas resulting from land abandonment processes. In addition, we tested the influence of densely wooded areas where habitat heterogeneity and shrub height were lower due to more intense management. We detected declines in insectivore bird abundance and functional divergence towards less managed areas. We also observed important declines in the community weighted means of ground-foraging, larger and long-billed species, which relate to the amount and diversity of pests consumed. Furthermore, Shannon–Wiener diversity slightly decreases responding to dense tree layer coupled with lower shrub height and habitat heterogeneity and this pattern is also followed by ground-foraging species that mostly have high wing aspect ratio. Finally, our results suggest that varying management intensity resulted in substantial changes in vegetation cover, height and overall habitat heterogeneity that drive differences in various dimensions of insectivore bird diversity with potential consequences for natural pest regulation in wood-pastures.

Keywords: wood-pasture; natural pest control; insectivore birds; functional diversity; effect traits; ecosystem services; montado/dehesa

Introduction

There is a growing body of research supporting the mechanistic relationship between biodiversity and ecosystem functioning and services (Brose and Hillebrand 2016). While higher species diversity has been associated with enhanced ecosystem functioning, this relationship is in large part regulated by the diversity of functional effect traits (i.e. the life-history characteristics of species associated with a particular ecological function) present in a community (Díaz and Cabido 2001; Lavorel and Garnier 2002; Díaz et al. 2007). One of the main hypotheses explaining the relationship between biodiversity and ecosystem functions is the mass-ratio hypothesis (Grime 1998; Garnier et al. 2004), which states that ecosystem functioning is mostly determined by the characteristics of dominant species in the community. For example, communities with more abundant insectivore species are likely to be more successful in controlling insect pest populations (Karp et al. 2013).

It should be noted however that a single trait is unlikely to provide a complete picture of how species affect ecosystem functions because multiple effect traits often interact to mediate the same function (Villéger et al. 2008; Gagic et al. 2015). For example, even if no differences are observed in the richness of insectivore species in a community, it is possible that a change in the functional diversity of traits associated with insect feeding, such as foraging behaviour or body morphology, may influence pest control functions in the ecosystem. This view is supported by the niche complementarity hypothesis, which states that higher functional diversity may enhance resource use efficiency and ecosystem functioning by promoting niche filling through multiple pathways (Hooper et al. 2005). According to this hypothesis, the efficiency of multiple ecosystem functions is mediated by differences

in niche occupancy between species, which are driven by their functional traits (Tilman et al. 1997; Loreau 1998). Thus, an increase in species richness is more likely to enhance ecosystem function if it also reflects an increase in functional diversity (Duncan et al. 2015), and the opposite is also true.

Because of the mechanistic links between functional traits and ecosystem functions, the analysis of functional diversity is better suited to explore changes in ecosystem functions than the analysis of taxonomic diversity (Cadotte et al. 2011; Gagic et al. 2015). The suite of methods used to analyse functional diversity have seen important developments in recent years, which have helped to elucidate the links between changes in environmental conditions, the composition of communities and their delivery of ecosystem services to humans (Mcgill et al. 2006; Flynn et al. 2011; Hevia et al. 2016). Ecosystem services are defined as the values and goods that humans obtain from ecosystems, including provisioning, regulation and maintenance, and cultural services and this conceptualisation of ecosystem services considers the whole range of ecological processes that shape the final provision of goods and services for human well-being (Millennium Ecosystem Assessment 2005). For instance, agricultural and forestry yields are often mediated by a number of other ecosystem services, including pest control, seed dispersal and pollination (Zhang et al. 2007; Bugalho et al. 2016; Moreno et al. 2018). The ever-growing human demand for food and material products has seen many production areas shift towards more intensive land uses, leading to concomitant changes in environmental conditions that may affect the functional diversity of species associated with these key services (Mace et al. 2012). Similar changes in the provision of ecosystem services may also occur when active land management is abandoned, which is increasingly happening in developed regions due to social and market dynamics, but the effects of land abandonment on ecosystem service provision have received less attention than those of land-use intensification (Cramer et al. 2008; Rey Benayas et al. 2007).

Traditional European wood-pastures are a key example of a socio-ecological system undergoing important transformations in management strategies in recent decades (Bergmeier and Roellig 2014). Wood-pastures have been historically managed to produce multiple timber and non-timber products but recent changes in the market price of commodities and the migration of people from rural to urban areas have left many such areas devoid of regular active human intervention (Bugalho et al. 2011; Levers et al. 2018). Abandoning grazing and other exploitation activities, which maintained the typical open character of wood-pastures, has led to important changes in the vegetation structure and spatial heterogeneity of these ecosystems which are likely to generate gains and losses for both species and ecosystem services (Lavorel et al. 2011; Lavorel et al. 2013). These dynamics need to be well understood if any potential negative consequences of land abandonment are to be minimized (Hatna and Bakker 2011; Queiroz et al. 2014).

Birds are one of the taxa that have remarkably high species richness in wood-pastures (Diáz et al. 1997; Telleria 2001; Catarino et al. 2016) and provide a range of ecosystem services (Whelan 2008; Rey 2011). Among these, pest regulation is often seen as an essential service provided by birds in wood-pastures given the substantial contribution of insectivore birds to control insect pests associated with trees and other commercially valuable plants (Phillpott et al. 2009; Kellermann et al. 2008; García et al. 2018). Birds are also good indicators of changes in the environment due to characteristics such as high mobility and conspicuousness (Konishi et al. 1989), making them an ideal group to study how changes in habitat structure and composition may influence the response of birds associated with insect predation (Mäntylä et al. 2011; Pereira et al. 2014). Previous studies have already explored how insectivore birds change in relation to habitat structure, and in some cases identified important mismatches between species and trait level responses with potential consequences for pest regulation

(Cumming and Child 2009). These results suggest that a combined assessment of taxonomic and functional diversity changes is necessary to obtain a more detailed picture of the consequences of environmental change for the provision of ecosystem services by birds.

In this study, we aimed to explore how the taxonomic and functional diversity of insectivore birds, given their potential contribution to insect pest control, respond to changes in habitat structure associated with different management strategies in wood-pastures across the Iberian Peninsula and North Africa, and how observed changes may be linked to the provision of ecosystem services. The main questions addressed in this paper are: **Q1)** Do the taxonomic and functional diversity of insectivorous birds respond to changes in habitat structure linked to land abandonment? **Q2)** How do individual effect traits associated with pest regulation vary in relation to habitat structure? We answer these questions by testing insectivore bird functional diversity and composition along a management gradient using a set of variables describing vegetation cover, height and heterogeneity.

Materials and Methods

Study Area

This study area covers a wood-pasture system widespread in the western Mediterranean, named *montado* in Portugal, *dehesa* in Spain and *azaghar* in some regions of North Africa (S1 Table). The annual temperature is around 11-18°C and the annual rainfall ranges between 410-910 mm in the study area (http://www.worldclim.org/). The sampled areas are dominated by cork oak (*Q. suber*), co-occuring with Algerian oak (*Q. canarensis)*, holm oak (*Q. rotundifolia)*, Pyrenean oak (*Q. pyrenaica*), stone pine (*Pinus pinea),* maritime pine (*P. Pinaster*) and shrub species such as strawberry tree (*Arbutus unedo*), rockrose (*Cistus* spp.), buckthorn (*Rhamnus alaternus*), and elmleaf blackberry (*Rubus ulmifolius*) in some areas. Grazing is often regular and commonly carried out by cattle, goat,

sheep and pig. Cork extraction is also a common land-use practice in the study area, besides tree cropping and pruning (Bugalho et al. 2009). Collection of mushrooms, pine nuts, wild berries, medicinal plants and beekeeping is rarely practised in some regions of Iberian Peninsula but still common in North Africa (Berrahmouni et al. 2007; Moreno and Pulido 2009).

Bird sampling

The point count method (Sutherland et al. 2004) was used to sample birds in thirty-seven wood-pastures across the Iberian Peninsula (17 in Portugal, 13 in Spain) and North Africa (7 in Morocco) during the spring of 2011. Because bird species assemblages are similar in Europe and North Africa wood-pastures (Correia et al. 2015), despite the geographical barrier of the Mediterranean sea, we were able to explore how birds respond to management strategies across both regions. The sampled wood-pastures had a minimum size of 50 hectares and distanced at least 10 km from each other. Fifteen counting stations, separated at least 200 m from each other and 100 m or more from the wood-pasture edge, were sampled in each wood-pasture. The sampling process in each station was performed twice, firstly during the early half (1 April to 15 May) and again during the late half (16 May to 20 June) of the breeding season. The same observer visited each station both times (one visit in the morning and one visit in the late afternoon for each area) and recorded all birds detected in a five-minute period, during times of peak bird activity and avoiding rainy and windy periods (Sutherland et al. 2004). Recently debarked areas were excluded from the sampling processes considering that some species may avoid those areas (Leal et al. 2011). The observer recorded all birds detected visually or acoustically and estimated the distance between the bird and the observer. Later, birds detected more than 100 m away from the observer and over-flying birds were excluded from the analysis since they may not be associated to the study area. The total abundance of each species in each wood-pasture area

was calculated by the maximum sum of individuals detected in the fifteen counting stations for any of the two visits since this represents the minimum number of birds present in the wood-pasture area (Bibby et al. 2005).

Trait data

Insectivorous birds play an important role in pest control in most ecosystems, including wood-pastures. To understand how changes in breeding bird communities may affect this ecological function, we selected bird species (S2 Table) that are mostly insectivore (over 50% of diet) during the breeding season (Cramp and Perrins 1998; Cramp and Simmons 2006; Walther and Jones 2008; Gosler et al. 2013; Craig et al. 2015; Collar 2015; Winkler et al. 2015; Storchová et al. 2018; Collar 2019; Hume and Kirwan 2019; Donald 2019; Gosler et al. 2019). Later, we collected data on five effect traits (Lavorel and Garnier 2002) that are closely associated to the arthropod consumption of insectivore birds: foraging substrate, body mass, bill length, tarsus length and wing aspect ratio. These effect traits were selected as indicators of trophic niche use as they relate to foraging location, the type and quantity of food resources consumed, and the mobility capacity of bird species, all of which can influence the ability and success of arthropod capture (Rey 2011; Luck et al. 2012; Hevia et al. 2016). All trait data is listed in S3 Table.

Foraging strata data were collected from the EltonTraits 1.0 database (Wilman et al. 2014). These data describe the percentage use of different foraging strata by bird species, including the ground, understory, mid-high and canopy. Foraging location provides information on how species utilize different habitat strata for resource acquisition (Holmes et al. 1990). Therefore, ground foraging species are expected to be more abundant in areas with more available open ground, in contrast to canopy, mid-high and understory foragers which may prefer more densely vegetated areas.

Bird body morphology was characterised based on three traits: body mass, bill length and tarsus length. Body mass data were also collected from the EltonTraits 1.0 database (Wilman et al. 2014). Body mass may indicate the quantity of food resources consumed in the habitat and is also associated with range size, as species with larger body mass have wider range sizes (Schoener 1968; Allen et al. 2006). Thus, larger species are expected to be more prevalent in actively managed wood-pastures, where a heterogeneous vegetation structure may provide more open areas. Moreover, the higher vegetation heterogeneity observed in these areas may also induce higher abundance or variety of arthropods (Horak 2014) which can benefit larger birds when compared to closed shrublands. Bill length data were collected from Cramp and Simmons (2006) and Storchová et al. (2018). Bill length related to the size and the type of feeding resources utilized as well as the foraging behaviour of the birds (Grant 1968; Pulliam and Enders 1971; Lederer 1975). Longer bills increase the ability of birds to probe the ground and small cavities for insects and likely associated with the capacity to feed on wide range of species and different life stages of pest species (Schoener 1971). In addition, information on tarsus length was also collected from Cramp and Simmons (2006) and Storchová et al. (2018). Tarsus length is closely associated with the foraging location of birds, as species with a shorter tarsus may have a physical advantage and better balance while foraging on the foliage and bark (Spring 1965; Norberg 1986) in contrast to longer tarsus which may facilitate locomotion in herb dominated areas (Schulenberg 1983). We expect foliage/bark gleaning species that have shorter tarsus to be more abundant in closed areas where woody vegetation is denser, in contrast to species with longer tarsus which may be highly prevented from those shrublands. Because these three traits are highly correlated, we performed a Principal Components Analysis (PCA) to avoid biased measurements of functional diversity (Lepš et al. 2006; Laughlin 2011; Mouillot et al. 2011). The first and the second dimensions of PCA (designated Body morphology – Axis 1 and 2 henceforth) were used as traits in subsequent

analyses (Table 1).

Finally, wing aspect ratio data were collected from multiple published resources or, when unavailable, were calculated based on available data for wingspan and wing area (Pennycuick 2008). All the references used to obtain wing measurements are presented in S4 Table. A higher aspect ratio is associated with better energy efficiency during flight, allowing birds to fly longer distances with a lower energetic cost (Tobalske 2007). In contrast, species with lower wing aspect ratio have better manoeuvrability in dense vegetation structures due to their shorter and rounder wings (Weis-Fogh 1973). We expect that species with lower wing aspect ratio will be more prevalent in closed shrublands, whereas species with higher wing aspect ratios will be associated with a more open habitat structure.

Table 1 PCA axis loadings of bird body morphology variables. First dimension (Axis 1) explains 78% of the variation indicating changes in tarsus length, bill length and body mass of insectivore birds across the study area. Second dimension (Axis 2) explaining 19% of the variation in body morphology variables which is majorly correlated to the bill length.

Body morphology variables	**Correlation of the variables to the PCA axes**	
	Axis1 (78%)	**Axis2 (19%)**
Tarsus length	0.611	0.404
Bill length	0.481	-0.872
Body mass	0.628	0.276

Habitat structure data

The variables used to characterize the habitat structure of each wood-pasture include understory cover and height, tree density and habitat heterogeneity. These variables were selected as representative of a management gradient ranging from active management (e.g. regular grazing, shrub removal, etc.)

to less managed (e.g. occasional grazing, no shrub removal) areas tending towards abandonment. Variables were estimated visually at each bird sampling station, including herb cover and shrub cover (% of ground cover), herb height (in 5 cm classes up to 25 cm) and shrub height (in 25 cm classes up to 150 cm) and then they were transformed in values up to 0.25 and 1.50 m, respectively. Tree density (number of trees per hectare) and canopy cover (% ground cover) were estimated visually from aerial images of the study area available from Google Earth v7.1. After that, a habitat heterogeneity index was calculated by applying the formula of "max. value – min. value/mean value" to each of the habitat variables defined above and then the resulting values were summed to obtain a single heterogeneity value for each wood-pasture (Rotenberry and Wiens 1980).

Subsequently, a Principal Components Analysis (PCA) was performed (Jolliffe 2002) using herb and shrub cover, herb and shrub height, tree density and habitat heterogeneity variables to avoid problems with correlation between variables (Dormann et al. 2013). The first and the second axis values of PCA were used as habitat management gradients in the analysis (Table 1). The first PCA axis is mostly associated with understory vegetation structure and development whereas the second PCA axis represents a gradient from sparsely wooded and more heterogeneous areas to densely wooded and less heterogeneous areas.

Table 2 PCA representation of the habitat variables used as management indicators. PC1 explains 46% of the variation majorly indicating herb and shrub cover changes throughout the study area. PC2, explaining 20% of the variation in the habitat structure, is mostly correlated to changes in habitat heterogeneity and tree density (number of trees per hectare).

Variables	Correlation of the variables to the PCA dimensions	
	Axis 1 (46%)	Axis 2 (20%)
Herb cover	-0.5735659	0.1074351
Tree density	0.2954380	0.5221969
Shrub cover	0.5675688	-0.1349756
Herb height	-0.3984235	0.1573461
Shrub height	0.2208402	-0.4852495
Heterogeneity	-0.2325783	-0.6613054

Data Analysis

We evaluated bird taxonomic diversity by calculating species richness, Shannon–Wiener diversity index (Shannon and Weaver 1949) and bird density (measured as the abundance of birds per hectare). We also calculated multi-trait functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve) indices to assess bird functional diversity. Functional richness (FRic) represents the number of traits in the community. Functional divergence measures the distance of highly abundant species to the centre of trait space of a community (Villéger et al. 2008). In other words, functional divergence increases if the most abundant species have very different trait assemblages (Mouchet et al. 2010; Laliberté and Legendre 2010). Moreover, functional evenness (FEve) shows the evenness of traits weighted by species abundances in the community (Mason et al. 2005). Contrary to FRic, FDiv and FEve indices are independent from species richness (Villéger et al. 2008). Before each index was calculated, we assessed the correlation between traits using Spearman correlations, since correlated traits can bias measurements of functional diversity. No significant correlations ($p>0.05$) were observed among traits (foraging strata, body morphology axis-1, body morphology axis-2 and wing aspect ratio), so all were included in the analyses, giving each trait an equal weight. To analyse the functional composition of birds, we calculated the community weighted

means (CWM) index of each trait to assess changes in the relative abundance of individual traits across the habitat structure gradient. For continuous traits, CWM values represent the mean value of that trait in the community representing their relative abundance (Lavorel et al. 2008).

We performed all analyses in R. 3.5.2 computing environment (R Core Team 2019). Taxonomic diversity indices, species richness and Shannon index were calculated using "specnumber" and "diversity" functions in "vegan" package (Oksanen et al. 2015). Functional diversity and functional composition indices were calculated using the 'dbFD' function in 'FD' package (Laliberté et al. 2014). We evaluated the relationship between taxonomic and functional indices and the habitat variables represented by PCA axes using generalized linear models implemented with the "glm" function in "stats" package. "rsq" package was used to record adjusted R-squared values for each model using "rsq" function in (Zhang 2018). We obtained the figures using "ggplot2" (Wickham et al. 2016).

Results

We observed a small increasing trend in species richness and a slight decreasing trend in Shannon diversity associated to the first axis representing habitat structure (Figure 1, Table 3), although both trends were non-significant. Similarly, a nearly significant decreasing trend was observed for Shannon diversity in relation to the second habitat PCA axis (Table 3). In addition, we detected nearly significant decreases in bird density (abundance of birds per hectare) from herb dominated areas to shrub dominated ones (Figure 1, Table 3).

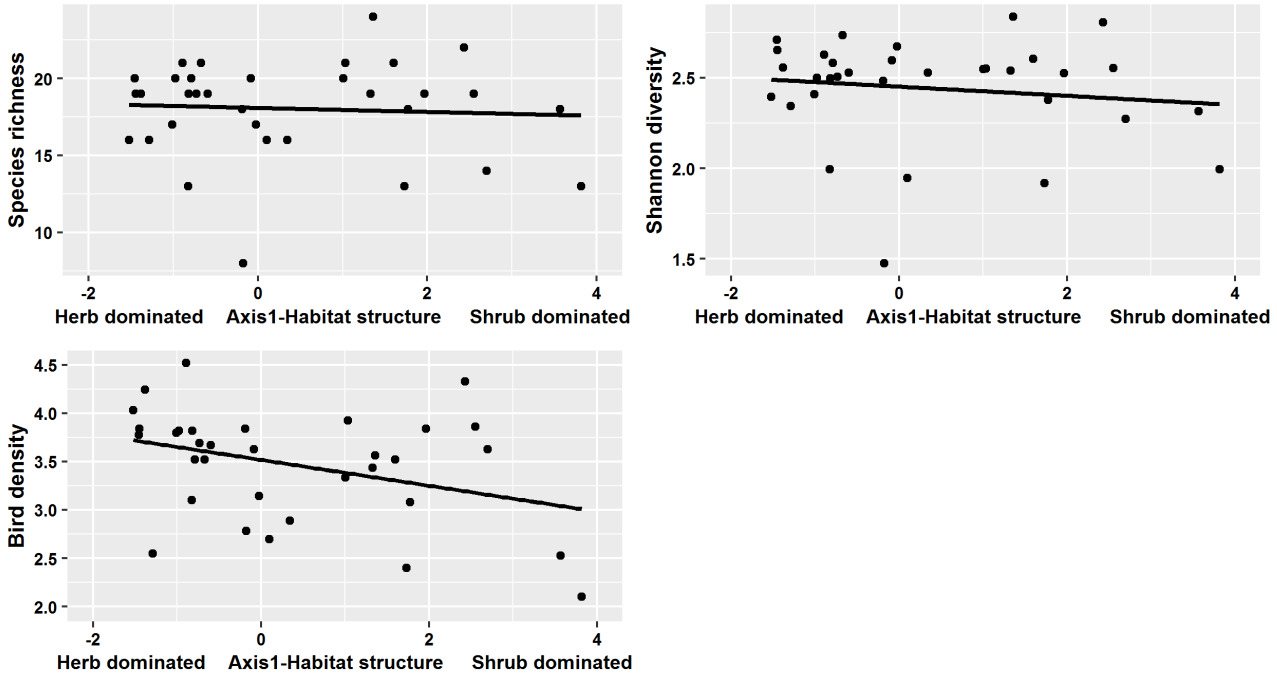

Fig. 1 Relation of species richness, Shannon diversity and density of insectivorous birds to the habitat structure represented by the first PCA dimension (Table 2). Species richness and Shannon diversity of birds did not significantly vary across the differences in habitat structure (p>0.05). The density of birds (abundance per hectare) decreased towards shrub dominated areas resulted as nearly significant. See Table 3 for test statistics of linear models.

Despite the lack of statistically significant changes in functional richness (FRic) and functional evenness (FEve), functional divergence (FDiv) significantly decreased towards areas with a lower intensity of management (Figure 2, Table 3). No significant associations were detected between any of the FD indices calculated and the second PCA axis (Table 3).

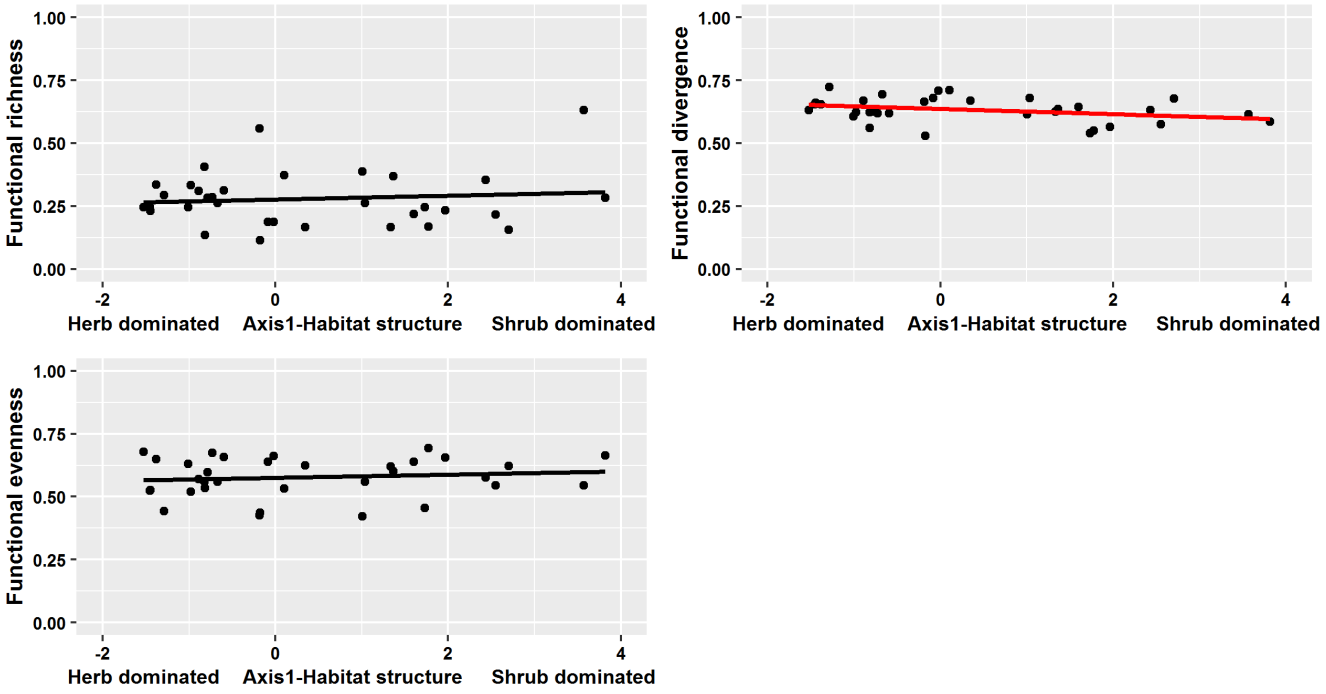

Fig. 2 Relation of functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve) of birds to the habitat structure (Table 2). Differences in functional richness and functional evenness across habitat structure are not significant (p>0.05). Functional divergence decreased towards shrub dominated areas where the management intensity is lower. We did not detect significant associations between FD indices and second dimension of PCA. See Table 3 for test statistics of linear models.

Table 3 Linear model results show the relation of species richness, Shannon diversity index and functional diversity indices to the habitat structure which are represented by the first and the second PCA dimensions (Table 1). The values in the table represent estimate, standard error (SE), significance level (p≤0.05) and adjusted correlation (R-squared) values resulted from the linear models.

Biodiversity indices	PCA Axis 1 (46%)				PCA Axis 2 (20%)			
	Estimate	SE	*p*	R^2	Estimate	SE	*p*	R^2
Intercept	17.689	0.533	<0.001		17.744	0.519	<0.001	
Species richness	0.177	0.316	0.57	0.02	-0.713	0.462	0.13	-0.036
Intercept	2.427	0.046	<0.001		2.431	0.044	<0.001	
Shannon diversity	-0.005	0.027	0.83	-0.03	-0.073	0.039	0.07	-0.064
Intercept	3.483	0.099	<0.001		3.479	0.103	<0.001	
Species density	-0.111	0.058	0.06	-0.07	-0.089	0.091	0.34	-0.001
Intercept	0.275	0.017	<0.001		0.276	0.017	<0.001	
Functional richness (FRic)	0.007	0.010	0.49	0.01	0.0005	0.016	0.97	-0.001
Intercept	0.639	0.008	<0.001		0.638	0.009	<0.001	
Functional divergence (FDiv)	-0.012	0.005	**0.02**	-0.12	-0.012	0.008	0.14	-0.031
Intercept	0.578	0.013	<0.001		0.578	0.012	<0.001	
Functional evenness (FEve)	0.004	0.008	0.62	0.02	-0.006	0.012	0.56	-0.018

We observed significant variations in the community weighted means (CWM) of traits representing foraging strata use, body morphology and wing aspect ratio of birds along the management gradient represented by the first PCA axis (Table 2). The CWM of ground-foragers significantly decreased towards shrub dominated areas, while canopy, mid-high and understory foraging species showed the opposite (Figure 3, Table 4). We also detected significant associations among these CWM indices and second dimension of PCA (Figure S1 , Table 4) showing increases in CWM of mid-high and understory foragers in contrast to decreases in ground foragers towards densely wooded and less heterogeneous areas where shrub cover and height is lower (Table 2).

The CWMs of both PCA axes associated with bird body morphology showed significant trends along the first PCA axis representing habitat structure (Table 2). The relative abundance of larger

species with longer bills and tarsus significantly decreased towards less managed areas (Figure 4, Table 4). In addition, the second PCA axis representing body morphology also increased significantly towards closed shrublands indicating a higher abundance of species with shorter bill size and longer tarsus in these areas (Figure 4, Table 4). We did not detect significant associations among these CWM indices and second dimension of PCA representing habitat structure. Finally, we observed significant changes in bird wing aspect ratio across (p=0.02; R2=-0.12) the second habitat structure PCA axis (Table 1). Wing aspect ratio reduced from sparsely wooded and more heterogeneous areas to less heterogeneous areas with dense woody vegetation **(**Table 4).

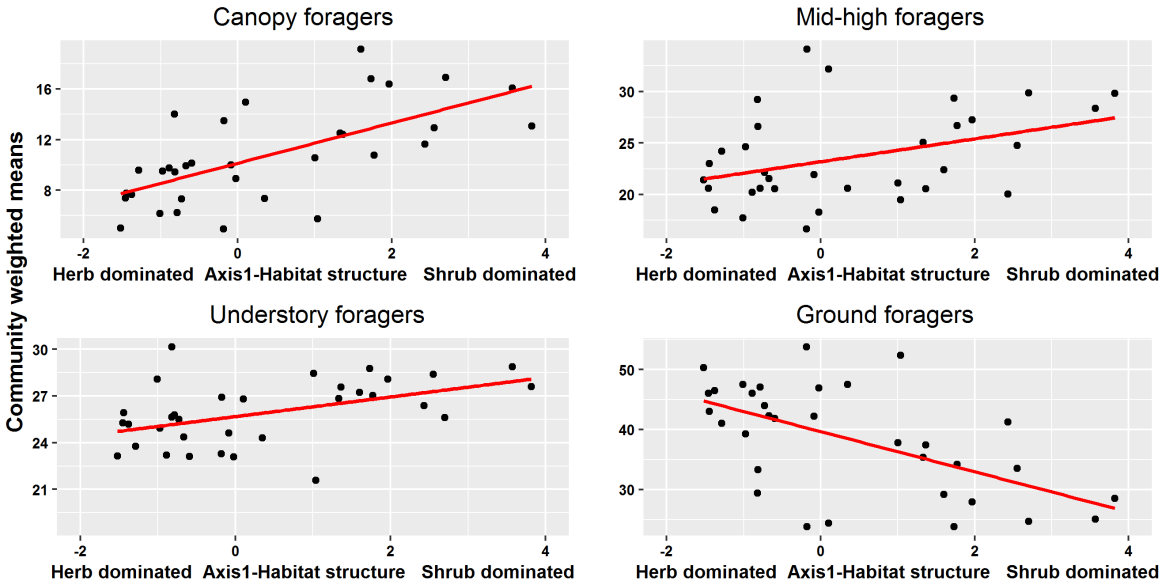

Fig. 3 Community weighted means (CWM) of foraging strata use of birds across the habitat structure from actively managed areas to less managed areas where shrub cover and height are higher. CWM of ground-foraging species severely declines towards less managed areas. However, canopy, mid-high and understory foragers increase from open areas to shrublands. See Table 4 for test statistics of linear models.

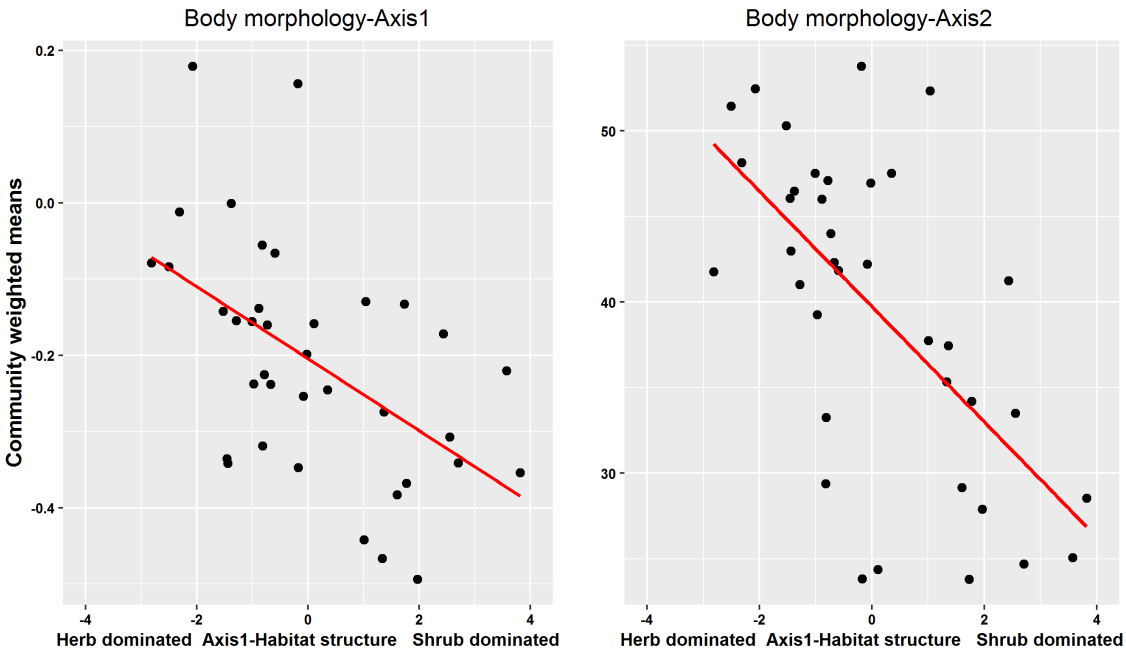

Fig. 4 Community weighted mean (CWM) of body size across habitat structure (Table 1). CWM of larger species, which represented with longer bill and tarsus length and higher body mass by the body morphology - Axis1 (Table 1), significantly decrease towards less managed areas. In addition, species with longer bill are more prevalent in managed, open areas although these species may have shorter tarsus and lower body mass as body morphology - Axis2 indicates (Table 1). See Table 4 for test statistics of linear models.

Table 4 Linear model results show the relation of community weighted means (CWM) values of traits to the habitat structure represented by the first and the second PCA dimensions. The table show estimate, standard error (SE), significance level ($p \leq 0.05$) and adjusted correlation (R-squared) values resulted from the linear models.

Traits	PCA Axis 1 (46%)				PCA Axis 2 (20%)			
	Estimate	**SE**	***p***	**R^2**	**Estimate**	**SE**	***p***	**R^2**
Intercept	10.214	0.453	<0.001		10.281	0.61	<0.001	
Canopy foraging	1.531	0.268	**<0.001**	0.46	0.731	0.548	0.19	0.021
Intercept	3.139	0.034	<0.001		3.140	0.034	<0.001	
Mid-high foraging	0.047	0.019	**0.02**	0.17	0.073	0.031	**0.02**	0.17
Intercept	25.61	0.358	<0.001		25.62	0.38	<0.001	
Understory foraging	0.650	0.212	**0.004**	0.19	0.700	0.339	**0.05**	0.082
Intercept	3.671	0.026	<0.001		3.676	0.026	<0.001	
Ground foraging	-0.088	0.016	**<0.001**	-0.37	-0.073	0.022	**0.001**	-0.11
Intercept	-0.204	0.021	<0.001		-0.206	0.025	0.001	
Body morphology-Axis 1	-0.040	0.012	**<0.001**	-0.25	-0.023	0.022	0.31	-0.001
Intercept	-0.033	0.016	0.05		-0.031	0.022	0.17	
Body morphology-Axis 2	0.057	0.009	**<0.001**	0.47	0.031	0.020	0.12	0.038
Intercept	5.402	0.024	<0.001		5.405	0.022	<0.001	
Wing aspect ratio	-0.008	0.014	0.54	-0.01	-0.049	0.020	**0.02**	-0.12

Discussion

Influence of management intensity on taxonomic and functional diversity patterns of insectivore birds

Our results show that habitat changes in understory cover, tree density and habitat heterogeneity associated with land abandonment induced changes in the taxonomic and functional diversity and composition of insectivore birds in wood-pastures. Although there were no significant changes in species and functional richness along the studied habitat gradients, we observed a slight decrease in the density (Fig. 1) and functional divergence (Fig. 2) of insectivore birds from actively managed wood-pastures towards less intensively managed areas dominated by shrubs (Table 3). Functional divergence

represents how dissimilar the abundance distribution of species is within the functional trait space of the community (Villéger et al. 2008; Mason and Mouillot 2008). We also observed a nearly significant reduction in Shannon diversity towards areas with higher tree density and less heterogeneity (Table 3). Overall, our results suggest that actively managed and heterogeneous wood-pastures tend to have more abundant and diverse insectivore bird communities.

Actively managed wood-pasture areas generally present an open and heterogeneous vegetation structure (Table 2), which is likely to increase niche diversity and facilitate the presence of species with different functional characteristics (Hartel et al. 2014; Tscharntke et al. 2008). Because these species will also have different ecological requirements, competition for resources is likely to be low which can partly explain the higher bird abundance observed in these areas. On the other hand, shrub-dominated and densely vegetated areas are less heterogeneous and consequently will have a lower diversity of niches available for insectivore bird species (Clavero and Brotons 2010). As expected, insectivorous bird species occupying these areas were more functionally similar to each other than in actively managed areas and bird abundance was lower, probably as a result of increased competition for resources. Interestingly, the functional homogenization of insectivorous birds in shrub-dominated and densely vegetated areas did not imply a reduction in species richness, which remained more or less constant across the studied habitat gradient. One possible explanation for this is that species richness may have remained stable along the habitat gradient as a result of species turnover, with species associated with resources that are less available or absent in densely vegetated areas likely being replaced by species that specialize in exploiting the resources available in these areas.

Several studies have already highlighted the existence of mismatches between species- and trait-level responses to environmental changes, particularly in human-shaped habitats (Cumming and Child 2009; Devictor et al. 2010; Seymour et al. 2015). Changes in land-use type and intensity lead to

variations in niche structure which may affect the functional diversity and composition of species assemblages independently of species richness and abundance (Arruda Almeida et al. 2018). This is because the functional traits that modulate species responses to the environment (i.e. response traits) may sometimes be independent of the traits that define species' contributions to ecological functions (i.e. effect traits) (Suding et al. 2008; Hevia et al. 2016). This emphasizes the importance of exploring the variation of response and effect traits to better understand the mechanistic relations of species and ecosystem processes under changes in habitat structure (Lavorel and Garnier 2002).

Functional diversity and composition unravel various dimensions of the relationship between species and environmental conditions that regulate the provision of ecosystem functions (Tilman et al. 1997; Mouillot et al. 2011). In the context of our results, the observed variations in functional divergence (FDiv) along the studied habitat gradient (Fig. 2, Table 3) suggest there may be important changes in the composition and abundance of individual traits along the gradient, with potential consequences for ecosystem functions. Indeed, our analysis of trait community weighted means detected compositional changes along the studied habitat gradient for multiple traits.

Functional composition of insectivore birds differentiates along with the management intensity

We detected significant changes in the composition of most traits towards shrub-dominated areas, and in foraging strata and wing aspect ratio along with the less heterogeneous areas with higher tree density. The community weighted means (CWM) of the proportional use of different foraging strata shows that canopy, mid-high and understory use increases towards areas with higher shrub cover and tree density (Table 4). These changes are expected due to the higher availability of feeding and nesting resources for canopy and shrub forager insectivore birds in habitats with higher woody plant cover (Barber and Marquis 2011; Barbaro et al. 2014), therefore particularly, mid-high and canopy foragers may prefer the higher niche availability provided by the dense tree layer in the study area.

Similarly, understory foragers may benefit from the remaining presence of a well-developed shrub layer shrub cover which is less declining compared to shrub height in these areas (Table 2). In contrast, ground foragers decrease significantly in the same areas. The availability of open habitats, which will be reduced in more densely vegetated areas, is one of the key factors driving the foraging activity and success of ground-foraging species (Wilson et al. 2005; Reino et al. 2010). Regular grazing controls shrub cover and height, which contributes to increase prey and predator detection and facilitate mobility for ground foraging birds (Vickery et al. 2001; Vickery et al. 2012; Leal 2019). Shrub or tree dominated areas may also induce several changes in shade rate, soil temperature, moisture (Peco et al. 2006; Castro and Freitas 2009) and which can decrease the availability of feeding resources for ground foragers by preventing the distribution of particular arthropods across different life stages (egg, larvae, pupae, imago) (Blaum et al. 2009) as well as regulate birds prey locating abilities by changing the light reflectance (Mäntylä et al. 2004; Mäntylä et al. 2008) that may finally decrease the feeding resource availability for ground foragers. Meanwhile, it should be noted that the decline of ground foraging activity is likely to be more severe than the changes observed in the CWM of understory foragers. This may happen because CWMs are calculated based on the average proportion of time that each species spends foraging on each stratum (Wilman et al. 2014), and this may hide more nuanced changes. Many ground-feeding specialists which carry out a lot of their feeding activity on the ground, such as Eurasian Thick-knee (*Burhinus oedicnemus*), Zitting Cisticola (*Cisticola juncidis*) and The Northern wheatear (*Oenanthe oenanthe*), were almost completely absent in shrub dominated areas and even species who are able to use multiple foraging strata are likely to be using upper vegetation strata more often than assumed in densely vegetated areas if vegetation development prevents ground foraging.

Significant changes in the morphology of insectivore bird species were also observed along the habitat structure gradient. The first PCA axis used to characterize bird species morphology showed a

negative trend along the habitat gradient associated with understory vegetation, suggesting that the abundance of species with longer bills and tarsus and higher body mass decreased towards less managed areas with a well-developed shrub layer (Fig. 4, Table 4). Larger species often have wide range sizes (Polo and Carrascal 1999; Allen et al. 2006) and longer tarsus facilitate locomotion in areas with patchy understory cover so these species may find it difficult to move into or within densely vegetated areas. On the contrary, shorter tarsus may provide better balance for smaller foliage and bark gleaning birds during the vertical foraging activity (Carrascal et al. 1990) and may allow these species to occupy more densely vegetated areas. Moreover, larger species often need to consume a higher abundance and variety of arthropods (Allen et al. 2006) that tend to be more available in heterogeneous vegetation structures maintained by non-intensive grazing (Engle et al. 2008; Fahrig et al. 2011).

Additionally, species with longer bills also tended to be more abundant in actively managed wood-pastures as suggested by both PCA axes associated with body morphology. Longer bills may facilitate the consumption of ground-dwelling arthropods, which often have life stages as egg, larvae or pupae buried in soil (Lederer 1975; Ceia and Ramos 2016), by ground-foraging birds. For example, ground-foraging species such as the Eurasian hoopoe (*Upupa epops*) (Battisti et al. 2000) and the Spotless Starling (*Sturnus unicolor*) are reported to effectively prey on buried imago, pupal and larval life-stages of several lepidoptera, sawfly, weevil, coleoptera and hymenoptera species, many of which are important pests species (Cramp and Perrins 1998). Furthermore, some understory or canopy forager insectivores such as Spotted woodpecker (*Dendrocopos major*), Golden Oriole (*Oriolus oriolus*) are among the long-billed species, which can feed on the pests in deep tree holes (Ceia and Ramos 2016), also have reduced abundance in less managed wood-pastures. Smaller and short-billed species, which are adapted for foraging in dense foliage also play important roles in consuming larvae and pupae of several pest species (Rey 2011; Ceia and Ramos 2016). The important role of Great Tit (*Parus major*)

and Blue Tit (*Cyanites caeruleus*) in controlling cork and holm oaks pests (Rabaça 1990; Santos 2002) as well as fruit pests has been widely reported in the literature (Solomon et al. 1976; Mols and Visser 2002). Lastly, wing aspect ratio also decreased in these densely wooded areas as our results indicate (Table 4). Species with a higher wing aspect ratio present longer and narrower wings, which reduce flight-cost, and are generally highly mobile but their presence and movements may be constrained in densely vegetated areas (Fernández and Lank 2007). In contrast, species with a lower wing aspect ratio have better manoeuvrability in dense vegetation structures and are therefore better adapted to densely vegetated habitats (Askew and Ellerby 2007).

Potential consequences of reduced management on natural pest regulation in wood-pastures

According to our results, changes in habitat structure associated with land abandonment may result in important consequences for pest control by birds in wood-pastures. Specifically, the observed reduction in insectivore bird abundance coupled with functional changes in foraging strata use and body morphology will likely drive simultaneous shifts in the amount and type of insects consumed by insectivorous birds in areas undergoing land abandonment. This assessment is supported by reports that a decrease in bird abundance is related to landscape elements and land-use changes leading to further changes in functional composition of birds in relation to type and amount of prey consumed (Karp et al. 2013; Barbaro et al. 2017). In wood-pastures, our results indicate the biggest shift associated with land abandonment is likely to be driven by the loss of larger, ground-feeding and long-billed bird species. As stated above, these species often feed on multiple life-stages of important pest species that either live on or are buried in the ground and predation pressure towards these pests will most certainly decrease in abandoned areas. Declines in natural pest control due to climate change impacts are predicted across Europe, and particularly in Mediterranean region (Civantos et al. 2012), but our findings indicate that land-use driven changes may be another factor threatening the provision of this important ecosystem

service provided by birds.

Regular and non-intensive grazing may be key to enhance pest control in wood-pastures as it is the main factor sustaining the semi-open and heterogeneous vegetation structure of wood-pastures, also controlling the encroachment of shrubs with high regenerative abilities (Almeida et al. 2015; Uytvanck van and Verheyen 2014). Grazing abandonment has been reported to positively influence species and trait assemblages of several taxa (Sebek et al. 2015; Horák et al. 2018a) as our results showed it for canopy and understory foraging birds. However, we also indicate the loss of particular bird guilds, mostly associated to the heterogeneous open habitats, in less managed, closed-canopied areas. Other studies have found similar negative influences of land abandonment on open habitat specialists, making it challenging to consider it as an opportunity to enhance biodiversity (Suarez-Seoane et al. 2002; Queiroz et al. 2014).

In this scenario, a moderate management strategy that preserves the semi-open and heterogeneous habitat structure of wood-pastures seems to be the most beneficial strategy to maintain functionally diverse communities. This is because the resources available for insectivorous birds in closed forests can often be preserved by maintaining patches of habitat where the shrub and tree layers are allowed to develop. It should also be noted that, according to our results, more intensely grazed and less heterogeneous areas may lead to reductions in insectivore taxonomic and functional diversity. Future research should aim to explore the multiple management strategies in more detail to identify those that ensure a better balance between economic and natural values in wood-pastures (Young et al. 2005; Plieninger et al. 2015). Regarding this, preserving natural predators of pests may substantially mitigate chemical use which induces water and soil pollution adversely affecting the whole ecosystem processes, besides its high costs to farmers (Mols and Visser 2002; Civantos et al. 2012). For instance, managing hedgerows has been recently shown to enhance the diversity of pest regulator species

reducing the need for chemical pest control (Morandin et al. 2014).

Especially considering the loss of larger ground foraging birds and the species with longer bills may indicate lower quantity as well as diversity of pests consumed in less managed areas (Schoener 1971; Beecher 1978). On the other hand, moderate management preserving semi-open and heterogeneous habitats highly favour ground forager insectivores, while still harbouring mid-high and understory foragers as it is evident from the changes in CWM values (Fig. 3) and higher functional divergence represented in these areas (Fig. 2). However, we should perform further evaluations on how to ensure the well-representation of short-billed species, which may have important role in pest regulation on foliage layer (Park et al. 2008; Leal et al. 2011), along with active management. Furthermore, intensely grazed, less heterogeneous areas also represented by the slight decreases in Shannon diversity (Table 3) possibly due to the loss of ground foragers with higher wing aspect ratio as our results indicate (Table 4). Overall, these results complementarily suggest that instead of abandonment or intensifying the grazing, a middle way in grazing regime that maintain habitat heterogeneity including each vegetation layer should be adjusted to ensure the presence of various bird guilds as well as ecosystem functions in the habitat.

To conclude, our results suggest that management strategies that are able to maintain habitat heterogeneity are more likely to host abundant and functionally diverse insectivore bird communities and may thus benefit from the role of these species as natural pest regulators. Nevertheless, we should note that the present study has the drawback of not having direct measured the efficiency of pest regulation by birds in areas with different habitat structure and management strategies. While the conclusions drawn from the observed results are plausible and supported by previous studies, future research should assess the impact of land-use changes on pest control by measuring insect predation pressure directly, and also on other ecosystem services and dis-services (Zhang et al. 2007; de Bello

2010; Bregman et al. 2016).

Conclusions

We used multiple biodiversity indices to explore the relationship between habitat structure and insectivore bird communities in wood-pastures and our results suggest that changes in vegetation structure and habitat heterogeneity driven by varying land-use intensity influence the taxonomic and functional diversity of insectivorous birds in Mediterranean wood-pastures. We observed a decline in bird density (abundance per hectare) in areas with denser vegetation and lower habitat heterogeneity as a result of reduced grazing pressure. We also observed a significant decrease in bird functional divergence in the same areas, mostly driven by a decrease in larger ground foraging birds. In contrast, smaller canopy-foraging birds seem favoured in less managed areas, although these species are abundant in regularly grazed areas. As a result, actively managed wood-pastures where canopy openness and heterogeneity are maintained seem to support more abundant and functionally diverse insectivore bird communities and may thus benefit from more effective natural pest regulation. Land-use changes may alter this balance, potentially leading to natural and economic value losses in wood-pastures (Kellermann et al. 2008; Landis et al. 2017). In order to preserve the healthy delivery of a wide range of ecosystem services in wood-pastures, future studies should also explore the complex dynamics associated with the provision of important ecosystem services by birds, such as seed dispersal and weed control, and how they may be influenced ongoing land use changes (Gonzalez-Gomez et al. 2006; de Bello et al. 2010).

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Table S1: Geographical coordinates of the central point of each wood-pasture area.

Sampling Areas		Latitude	Longitude
1	Portugal	41.50872	-7.074138
2	Spain	41.18415	-5.80492
3	Spain	41.17614	-5.74195
4	Spain	40.19319	-6.24296
5	Spain	39.55685	-5.38128
6	Spain	39.622	-7.40766
7	Spain	39.22826	-6.56217
8	Spain	37.3366	-6.51521
9	Spain	37.26132	-6.47627
10	Portugal	38.58572	-8.09225
11	Spain	36.77316	-5.2837
12	Spain	36.59106	-5.3828
13	Spain	36.30048	-5.43845
14	Morocco	34.18165	-6.57416
15	Morocco	34.14664	-6.66846
16	Morocco	34.04243	-6.537
17	Morocco	33.9868	-6.50113
18	Portugal	37.24968	-7.86414
19	Portugal	37.30638	-8.08284
20	Portugal	37.41838	-8.08052
21	Portugal	37.76855	-8.59344
22	Portugal	38.34107	-8.42914
23	Portugal	38.44052	-8.5779
24	Portugal	38.10148	-8.58572
25	Portugal	39.25958	-8.28124
26	Portugal	37.71144	-8.3687
27	Portugal	39.01462	-8.13397
28	Morocco	34.05619	-4.2629
29	Morocco	35.17759	-5.34517
30	Morocco	35.1247	-5.2828
31	Portugal	39.22419	-7.45079
32	Portugal	39.33717	-7.59073
33	Spain	40.25066	-6.21399
34	Spain	40.08948	-6.5715
35	Portugal	38.38063	-7.8978
36	Portugal	38.68892	-8.3348
37	Portugal	38.82376	-8.8237

Table S2: Insectivore bird abundance data.

Sampling Areas	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
	Portugal	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Spain	Portugal	Spain	Spain	Spain	Morocco	Morocco	Morocco	Morocco	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Portugal	Morocco	Morocco	Morocco	Portugal	Portugal	Spain	Spain	Portugal	Portugal	Portugal
Aegithalos caudatus	3	0	0	1	2	0	0	0	0	2	0	4	2	0	0	0	0	0	0	5	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Burhinus oedicnemus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	2	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Certhia brachydactyla	16	9	19	18	18	11	20	3	4	16	15	16	14	0	1	0	1	14	6	13	10	13	14	14	15	18	15	14	2	4	23	19	13	18	18	18	5
Cisticola juncidis	0	0	0	0	0	0	0	2	10	8	0	0	0	0	0	0	0	0	9	0	14	0	0	0	1	2	2	0	2	1	2	2	0	0	0	0	10
Cuculus canorus	2	9	4	4	0	5	0	6	1	3	0	2	2	0	0	0	0	0	2	3	3	4	2	3	3	2	1	1	0	0	4	3	4	6	3	3	0
Dendrocopos major	3	3	2	1	4	5	2	0	2	4	7	6	4	20	13	23	12	3	10	6	6	3	8	6	4	8	4	5	3	11	2	4	5	0	2	2	8
Fringilla coelebs	21	38	46	42	46	39	46	6	23	19	32	37	27	62	41	47	41	26	19	23	28	41	41	22	37	26	35	33	24	20	45	59	42	38	36	20	49
Hippolais polyglotta	1	0	1	1	0	0	0	0	1	2	0	1	0	0	0	0	0	1	2	0	3	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Jynx torquilla	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Luscinia megarhynchos	16	14	5	1	4	7	0	0	3	15	2	0	5	0	0	0	0	8	12	6	6	0	6	6	6	3	8	0	1	2	3	1	3	6	8	5	8
Lullula arborea	6	12	24	19	4	18	25	1	6	15	2	4	0	0	2	5	1	6	17	26	15	15	3	22	8	24	17	1	0	1	23	15	14	16	7	17	6
Lanius senator	0	11	9	15	1	11	14	20	2	0	0	0	0	0	1	0	0	0	0	1	1	4	0	2	1	12	1	0	0	0	10	1	9	14	13	5	0
Muscicapa striata	0	0	0	4	0	0	0	0	0	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3	0	0	0
Oenanthe oenanthe	0	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oriolus oriolus	6	2	3	3	3	2	1	0	3	0	0	0	6	0	1	0	0	6	6	3	1	5	0	5	0	7	0	8	1	1	0	6	14	5	3	0	0
Cyanistes teneriffae/Parus teneriffae	0	0	0	0	0	0	0	0	0	0	0	0	0	25	33	28	26	0	0	0	0	0	0	0	0	0	0	28	19	28	0	0	0	0	0	0	0
Cyanistes caeruleus/Parus caeruleus	13	17	18	15	13	22	19	9	16	25	19	20	21	0	0	0	0	23	14	26	19	24	23	13	23	21	19	0	0	0	18	19	15	11	23	18	10
Parus major	10	6	12	12	11	10	8	15	20	12	21	20	11	15	17	15	8	9	8	11	10	15	7	9	8	10	6	26	17	12	9	7	10	7	11	8	7
Phylloscopus bonelli	8	15	11	0	2	0	0	0	0	0	11	14	13	0	0	1	6	0	0	0	1	1	5	0	9	0	2	10	2	1	0	1	2	0	1	0	2
Phoenicurus phoenicurus	2	7	8	0	4	0	1	0	0	7	0	0	0	0	1	0	2	2	0	4	9	1	16	16	8	5	6	0	0	0	0	0	0	0	1	0	0
Phylloscopus ibericus	1	0	0	0	0	0	0	4	0	3	2	9	3	0	0	0	0	11	0	2	2	4	2	1	11	0	1	0	1	0	0	0	0	0	0	0	0
Lophophanes cristatus/Parus cristatus	3	1	0	0	7	2	2	0	0	0	3	3	11	0	0	0	0	1	0	1	0	0	1	9	0	1	0	0	0	4	1	0	0	0	0	3	3
Regulus ignicapilla	2	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sturnus unicolor	5	10	16	14	6	21	20	11	14	4	9	1	2	0	1	7	7	1	8	12	14	13	10	13	2	35	15	0	0	0	14	37	15	25	16	12	30
Sitta europaea	9	11	6	1	6	6	13	0	1	19	9	15	5	0	2	0	0	4	6	9	13	19	19	6	7	12	11	18	0	1	12	12	6	4	15	8	9
Saxicola rubicola/Saxicola torquatus	1	3	1	2	0	0	0	0	0	2	6	0	0	2	1	1	0	4	5	2	9	2	2	6	2	0	7	1	0	0	0	0	1	0	2	4	13
Sylvia cantillans	4	6	1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Sylvia undata	0	7	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	5	0	0	1	0	0	0	0
Troglodytes troglodytes	17	1	0	0	2	0	0	0	0	8	15	11	15	0	0	0	0	23	11	3	9	1	6	3	5	2	3	3	7	4	0	0	0	0	1	4	10
Turdus merula	14	13	9	14	10	8	14	6	12	16	22	13	20	2	3	3	1	11	11	14	5	6	13	6	11	6	7	15	19	18	13	3	12	8	7	6	6
Turdus viscivorus	2	5	8	3	2	1	5	0	0	0	3	2	1	4	3	5	2	2	0	1	0	1	0	2	0	1	2	8	0	4	3	3	0	1	1	0	0
Upupa epops	3	4	9	5	0	11	9	10	2	1	0	0	0	0	0	0	7	0	1	0	0	0	6	0	0	0	5	4	0	0	0	8	3	4	16	6	3	1

Table S3: Trait data of insectivore birds.

Species	Wing aspect ratio	Body morphology-Axis 1	Body morphology-Axis 2	Foraging strata-Ground	Foraging strata-Understory (below 2m)	Foraging strata-Mid high (above 2m)	Foraging strata-Canopy
Aegithalos caudatus	4.94	-1.16805480914668	0.55916401043754	10	40	10	40
Burhinus oedicnemus	7.36	7.30953453467573	1.50136799520025	80	20	0	0
Certhia brachydactyla	7.22	-0.738352143204269	-0.383091248522812	40	30	30	0
Cisticola juncidis	2.7	-0.806541437188987	0.243383789471207	100	0	0	0
Cuculus canorus	6.51	0.943168335681457	-0.636823650471846	20	20	40	20
Dendrocopos major	4.02	0.785394735371697	-0.75699598855691	0	20	40	30
Fringilla coelebs	5.66	-0.614320056181339	-0.008423749923746	40	30	30	0
Hippolais polyglotta	6.89	-0.5245591994684	-0.02364611617431	0	40	20	40
Jynx torquilla	4.51	-0.392445136136778	0.004475076411498	60	20	20	0
Luscinia megarhynchos	5.17	-0.020103891821833	0.138053696382634	70	30	0	0
Lullula arborea	4.95	-0.390960721614698	0.182025128817846	100	0	0	0
Lanius senator	5.63	0.022069180635524	-0.030927888395912	100	0	0	0
Muscicapa striata	5.24	-0.83506342879965	-0.194915404971662	60	40	0	0
Oenanthe oenanthe	5.36	0.037309327983812	0.141939844841287	100	0	0	0
Oriolus oriolus	7.55	0.74498468513192	-0.748443049480254	0	0	0	50
Cyanistes teneriffae/Parus teneriffae	6.02	-1.03390877420647	0.455024173248755	0	33	33	33
Cyanistes caeruleus/Parus caeruleus	6.02	-1.02032726910417	0.458790228899306	10	30	30	30
Parus major	4.57	-0.650642433338389	0.281948659095638	0	20	60	20
Phylloscopus bonelli	4.63	-0.810393745521458	0.183364977971371	0	20	0	80
Phoenicurus phoenicurus	4.78	-0.468877758516243	0.151654693381297	20	40	40	0
Phylloscopus ibericus	2.8	-0.9135881317476	0.164104143746574	25	25	25	25
Lophophanes cristatus/Parus cristatus	6.7	-0.852289287800819	0.314430237650786	10	10	20	60
Regulus ignicapilla	4.21	-1.00783598687977	0.245132415750576	0	50	50	0
Sturnus unicolor	5	1.28434921904052	-0.568993817316831	50	50	0	0
Sitta europaea	5.49	-0.266339350727746	-0.399638973189163	33	33	33	0
Saxicola rubicola/Saxicola torquatus	4.88	-0.457900444369246	0.244155912092405	100	0	0	0
Sylvia cantillans	4.81	-0.742628052558807	0.190392515065348	10	20	60	10
Sylvia undata	4.81	-0.720936970327138	0.214718864197997	0	100	0	0
Troglodytes troglodytes	5.26	-0.811978043081589	0.049167344763294	50	50	0	0
Turdus merula	4.42	1.01952600386554	0.670198907112866	60	20	20	0
Turdus viscivorus	5.59	1.02214773346403	0.827694634252653	60	20	10	10
Upupa epops	5.01	2.07956331589184	-3.46928736178767	100	0	0	0

Table S4: References used to obtain/calculate wing aspect ratio.

Species	References
Aegithalos caudatus	[1]
Burhinus oedicnemus	[2]
Certhia brachydactyla	[4], [8], [9]
Cisticola juncidis	[5], [8], [9] (Cisticola)
Cuculus canorus	[1]
Dendrocopos major	[1]
Fringilla coelebs	[1]
Hippolais polyglotta	[3], [8], [9]
Jynx torquilla	[1]
Luscinia megarhynchos	[1]
Lullula arborea	[4], [8], [9]
Lanius senator	[6], [8], [9]
Muscicapa striata	[1]
Oenanthe oenanthe	[4], [8], [9]
Oriolus oriolus	[7], [8], [9]
Cyanistes teneriffae/Parus teneriffae	[1]
Cyanistes caeruleus/Parus caeruleus	[1]
Parus major	[1]
Phylloscopus bonelli	[6], [8], [9]
Phoenicurus phoenicurus	[1]
Phylloscopus ibericus	[1] (Phylloscopus collybita)
Lophophanes cristatus/Parus cristatus	[4], [8], [9]
Regulus ignicapilla	[1]
Sturnus unicolor	[2]
Sitta europaea	[1]
Saxicola rubicola/Saxicola torquatus	[1]
Sylvia cantillans	[6], [8], [9] (Sylvia undata)
Sylvia undata	[6], [8], [9]
Troglodytes troglodytes	[1]
Turdus merula	[1]
Turdus viscivorus	[1]
Upupa epops	[1]

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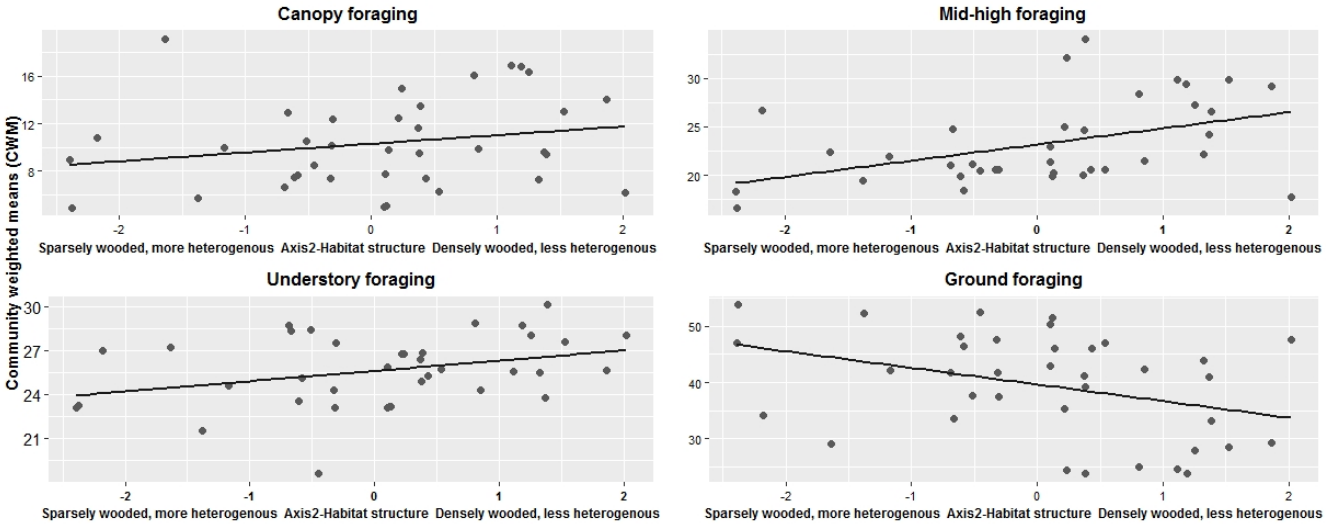

Figure S1. Community weighted means (CWM) of foraging strata use of birds across the habitat structure from sparsely wooded and more heterogeneous areas to densely wooded and less heterogeneous areas where shrub cover and height is lower (Table 2). CWM of mid-high and understory foragers are higher in densely wooded areas, whereas CWM of ground-foraging species reduce towards these less heterogeneous areas. See Table 4 for test statistics of linear models.

CHAPTER 6

General Discussion

Wood-pastures are complex social-ecological landscapes that have economic value resulting from the multi-functional human-use, which has also shaped a heterogeneous habitat structure (Rackham 2013). They often harbour very diverse species assemblages (Bergmeier and Roellig 2014), but are threatened by land abandonment and intensification that transforms multi-functional, heterogeneous habitats into homogeneous areas (Plieninger et al. 2015). The main challenge in conserving wood-pastures is to find optimal ways to manage their pasture and the woody components to balance their natural and economic values sustainably (Hartel and Plieninger 2014b). For this aim, it is crucial to provide scientific evidence that supports the development of biodiversity-friendly management strategies in wood-pastures (Jakobsson 2018).

This thesis explores species and trait level biodiversity patterns of plants, beetles, lichens (Chapter 2 and 3) and birds (Chapter 4 and 5) across different habitat structures of Iberian and North African wood-pastures that are driven by various management strategies. The ultimate aim of this work was to contribute to the development of low-cost management strategies to sustain biodiversity-rich habitats and potentially stimulate ecosystem functioning and ecosystem services in wood-pastures. The following sections present the key findings and limitations of the previous chapters (Chapters 2 - 5) and summarize the main management recommendations arising from it.

Importance of habitat heterogeneity

Environmental heterogeneity is one of the major factors driving species occurrence and diversity (Benton et al. 2003; Tscharntke et al. 2012). Spatial heterogeneity increases species diversity by

facilitating mechanisms of coexistence, persistence and diversification of species in the habitat (Tews et al. 2004; Stein et al. 2014). Higher environmental heterogeneity enhances potential niche space, including the availability of feeding resources, nesting, breeding and shelter as well as different abiotic conditions such as soil nutrient availability, shade rate and micro-climatic diversity, which contribute to increase the number of species that can coexist (Currie 1991; Erdős et al. 2018b). A higher diversity of niche components also facilitates the persistence of species with various ecological requirements and lowers extinction risk from environmental perturbations (Seto et al. 2004). Lastly, environmental heterogeneity stimulates the likelihood of diversification among species and within species, increasing the pathways of niche utilization and thereby ecosystem functions and services (Antonelli and Sanmartin 2011).

Despite some observations of hump-shaped, non-significant or even negative relations between spatial heterogeneity and biodiversity, mostly related to the specific adaptation of species due to their sensitivity to habitat continuity or related to the species having narrow niche width, recent studies have detected a general tendency for positive effects due to higher habitat heterogeneity (Tews et al. 2004; Hortal et al. 2013; Stein et al. 2014). Stein et al. (2014) also clarified the multiple terms that have been used to define environmental heterogeneity referring to both the biotic (habitat or vegetation diversity) and abiotic (diversity of climatic conditions, soil type and topographic structure) components of spatial heterogeneity. Habitat heterogeneity, which is the second most common term in the literature, refers to the variation within and between habitat variables and represents the major differences in vegetation structure across different dimensions, such as plant diversity and complexity (Stein et al. 2014). Thus habitat heterogeneity can be represented by various indices such as taxonomic and functional plant diversity and composition as the results of Chapters 2 and 3 indicate or height or cover of herbaceous, shrub and tree layers or PCA representation of multiple habitat variables (Kolasa and Rollo 1991; Stein

et al. 2014), which is applied in Chapters 4 and 5. The diversity and complexity of vegetation comprising the main structure of the habitat shape the primary niche components such as feeding and nesting resources, or shelter and refuge sites. It may thus also drive the trophic interactions and ecosystem processes and influence the presence and abundance of species (Tews et al. 2004; Kadmon and Allouche 2007; Gil-Tena et al. 2007).

Human-modified habitats are often associated with high level of man-made habitat heterogeneity, but in recent years land-use driven declines in mosaic habitat structure have been reported for wood-pastures (Plieninger et al. 2015; Hartel et al. 2015). Therefore, further studies are needed to better understand the influence of habitat heterogeneity on biodiversity and the associated ecosystem functions, particularly in threatened wood-pastures (Martins et al. 2014)

The role of shrubby patches increasing spatial heterogeneity and biodiversity value of wood-pastures

Wood-pasture landscapes are often comprised of various semi-natural elements, such as riparian galleries, olive orchards, hedgerows and shrubby patches that greatly contribute to the spatial heterogeneity of the landscape. Shrubby patches within the wood-pasture matrix are usually dotted with rocks that naturally protect them from mechanical shrub removal. As time passes, the shrub layer becomes progressively denser, making the access to grazers increasingly difficult. This allows the growth of native shrubs, such as broom (*Cytisus* spp. and *Retama* spp.), buckthorn (*Rhamnus alaternus*), elmleaf blackberry (*Rubus ulmifolius*), rockrose (*Cistus* spp.), tree heath (*Erica arborea*), lavender (*Lavandula* spp.), myrtle (*Myrtus* spp.), gorse (*Ulex* spp.) and hawthorn (*Crataegus monogyna*). In contrast, in the surrounding grazed areas the vegetation is mostly limited to tree and herb layers, especially in more intensively grazed areas (Garbarino and Bergmeier 2014). The role of shrubs in enhancing feeding, shelter and nesting opportunities has been widely reported for a variety of

taxa (Doblas et al. 2009; Azul et al. 2011; Hartel et al. 2014). Moreover, shrubs can enhance micro-habitat diversity by altering the temperature, humidity, shading and soil nutrient composition, stimulating the presence of distinct species with various niche requirements (López-Pintor et al. 2006; Simões et al. 2009). The presence of particular shrub species, such as *Retama sphaerocarpa*, is also reported to support young oak seedlings by preventing the extensive herb growth which induce water competition in the habitat (Cuesta et al. 2010).

Chapter 2 and Chapter 3 provide additional evidence supporting the contribution of shrubs to enhance overall woody vegetation diversity, and to broaden the range of niches available to other taxa in wood-pastures. A higher presence of shrubs in addition to trees and rocks within the small patches supported more diverse species assemblages of beetles and lichens and significantly increased the overall richness of plants, beetles and lichens in wood-pastures, as we demonstrated in Chapter 2. Our results are consistent with previous reports showing an influence of non-cropped and ungrazed areas in driving distinct species composition patterns and stimulating species diversity (Freemark and Kirk 2001; Benton et al. 2003; Bugalho et al. 2011b; Listopad et al. 2018). Furthermore, Chapter 3 reveals that these distinct species assemblages of plants, beetles and lichens found in shrubby patches also represent functional groups different from those found in the wood-pasture matrix. Ungrazed patches harbour a higher relative abundance of evergreen, woody, broad-leafed, fleshy-fruited and zoochory-dispersed plants due to the greater presence of shrubs, whereas the adjacent grazed matrix is mainly dominated by linear-leafed, deciduous herb forms. These differences in vegetation structure are reflected in the trait composition of beetles and lichens assemblages. Shrubby patches tend to have more small-sized and fungivore beetles as well as fruticose, foliose-broad, hygrophytic and oligotrophic lichens than the matrix. On the other hand, the wood-pasture matrix has a slightly higher abundance of macropterous beetles, which benefit from the availability of open habitats, and a significantly higher relative

abundance of foliose-narrow, xerophytic and nitrophytic lichens.

The contrast of functional groups of beetles and lichens present in patches and the matrix suggest that shrubs not only enhance feeding and nesting resources, but also provide distinct environmental conditions, increasing the niche diversification in the habitat. For example, the higher presence of fungivore beetles and hygrophytic lichens suggests that stimulating the regeneration of the shrub layer may provide more humid micro-habitats in the wood-pastures, which are crucial for several species, especially during the drier seasons (Breshears 2006). Moreover, the observed differences in the level of tolerance to eutrophication of lichens found in patches and the matrix indicate a possible role of livestock grazing in driving nutrient availability in wood-pastures (Hamilton and Frank 2001). The observed differentiation in lichen growth forms in response to variations in moisture or nutrient availability also supports the role of shrubs in providing specific niches in wood-pastures. Furthermore, as reported for hedgerows (Lecq et al. 2017), shrubby patches may enhance habitat connectivity for smaller beetles by supporting the maintenance of metapopulation networks, although this possibility was not studied here. In addition, our results indicate that herbivore beetles are not only constrained by niche availability in shrubby patches, but they can also benefit from host plant availability in the wood-pasture matrix. Similarly, predators and saprovore beetles seem to benefit from the niche availability of both patches and the matrix.

Moreover, the differences observed in the trait assemblages of plants, beetles and lichens resulted in higher functional dispersion for plants and higher functional evenness for beetles and lichens in the shrubby patches compared to wood-pasture matrix (Chapter 3). The higher functional dispersion of plants in patches arises from the appearance of new and distinct traits associated with the presence of woody plants, as detailed above. Functional evenness, which is a rarely tested index in the literature when compared to functional richness or dissimilarity indices (Mouillot et al. 2005), was higher for

beetles and lichens in patches than in the matrix, potentially indicating a more regular niche filling in patches (Hillebrand et al. 2008; Crowder et al. 2010; Gerisch et al., 2011). The substantial differences observed in the trait compositions of beetles and lichens might also indicate a difference in functional dissimilarity patterns. However, our results suggest that the level of dissimilarity is more or less same for both patches and matrix, even though these two habitat components are represented by distinct trait assemblages.

Finally, the results presented in Chapters 2 and 3 also highlight the advantages of analysing multi-taxa, particularly if including less studied taxa, to explore the sensitivity of different species to grazing-induced changes in habitat. The inclusion of multiple taxa in our functional diversity assessments allowed us to characterize various ecological features of shrubby patches and the wood-pasture matrix. The results of this assessment provide evidence of the advantages of allowing shrub regeneration in very small patches to enhance habitat heterogeneity in wood-pastures. Considering the mechanistic link of functional diversity and ecosystem processes, the higher functional dissimilarity of plants and higher functional evenness of beetles and lichens observed in patches highlights their contribution to enhanced ecosystem functioning, as well as to ecosystem services provided by these taxa (Lavorel et al. 2013a).

Consequences of land-use changes on biodiversity, ecosystem functioning and services in wood-pastures

Chapters 4 and 5 focused on exploring habitat structure at larger spatial scales and along a management gradient ranging from active management toward land abandonment. Principal Components Analysis was used to summarize various vegetation structure dimensions and allowed the characterization of the effects of land-use changes in two dimensions. Firstly, we explored the influence of higher density of shrub cover and height coupled with lower habitat heterogeneity resulting from severely reduced management intensity. Secondly, we evaluated the impact of more intense management, which highly

reduce the shrub height and shrub cover together with overall habitat heterogeneity, while maintaining the higher tree density. The management that is referred in this work consists in grazing, mechanical shrub removal, active tree plantation and pruning, all contributing to substantial differences in vegetation cover, height and overall habitat heterogeneity.

As shown in Chapter 4, widespread shrub development and lower vegetation heterogeneity in the habitat did not significantly influence the taxonomic richness and diversity of breeding birds in Iberian and North African wood-pastures. However, these changes in vegetation structure do restrict the occurrence of particular functional groups and induce declines in functional dissimilarity and functional evenness of birds. A habitat structure associated with a reduced management intensity restricts the occurrence of granivore, ground-nesting and ground-closed foraging species which are the major functional identities of grassland birds. Thereby, our results support previous findings (Russo 2007; Moreira and Russo 2007; García-Tejero et al. 2013) revealing the negative influences of land abandonment on open-habitat specialists due to the loss of semi-open habitat and of the related primary niche spaces required by these species. On the other hand, we observed that specific forest birds, especially arboreal nesting birds and canopy and shrub foragers benefit from the higher density of woody vegetation, as might be expected (Sirami et al. 2007; Jakobsson 2018), although the latter stages of land abandonment may be poorer in some feeding resources such as plants (Kesting et al., 2015) and insects (Balmer and Erhardt, 2000). Furthermore, it should be noted that regularly managed areas where habitat heterogeneity is preserved do not greatly restrict the occurrence of these forest-associated species (Chapter 4). Lastly, there may be some risks associated to large continuous areas of high shrub, such as increasing severity of wildfires, invasion risk and loss of trophic links that may be eventually

detrimental for biodiversity and ecosystem functioning of wood-pastures. (Russo 2007; Plieninger et al. 2014).

Chapter 5 focused on a specific feeding guild, insectivore birds, and presents further insights on the effects of land-use driven changes in habitat structure on taxonomic and functional diversity of breeding birds in Mediterranean wood-pastures. Insectivore bird density (bird abundance per hectare) declined towards shrub-dominated areas, whereas species richness and diversity remained more or less stable along the studied habitat structure gradient. Following the slight declines in abundance pattern, the functional divergence of insectivore birds also decreased towards less managed areas, where the understory is mostly dominated by shrubs and habitat heterogeneity is lower. In this chapter, functional evenness of insectivore birds was stable across the management intensity gradient in contrast with the results of Chapter 4. This may indicate that the abundance distribution of trait assemblages in less managed wood-pastures, which are mainly composed of canopy, understory, midhigh foragers and short-billed birds, are evenly distributed in these areas. However, these trait assemblages are represented with lower functional divergence because of the limited availability of ground-forager insectivores, resulting in reduced functional diversity in less managed wood-pastures.

These decreases were mostly driven by changes in the relative abundance of insectivore species with specific foraging strata preference and body size characteristics, traits that are closely associated to the quantity as well as type of arthropods consumed by these birds and therefore important in pest regulation. We observed a severe reduction of ground foraging insectivore birds coupled with declines in species with higher body mass, longer tarsus and longer bills towards less managed areas. In addition, species with high wing aspect ratio, together with ground foraging birds, negatively responded to increasing tree density and lowering shrub height and habitat heterogeneity. This emphasizes that the natural pest regulation may be highly influenced by canopy closure and the loss of

mosaic habitat structure. On the other hand, in line with the findings in Chapter 4, canopy and shrub forager insectivore birds can still benefit from the more heterogeneous, managed areas, given that their relative abundances were not severely decreased.

In summary, our results show the contribution of non-intensive, regular management in maintaining habitat heterogeneity, which support taxonomically and functionally diverse communities of birds in wood-pastures (Chapters 4 and 5). The major threats to these systems are changes in land-use regimes inducing either the abandonment of regular grazing or intensive exploitation leading to overuse, both of which cause substantial changes in the vegetation structure, canopy openness and habitat heterogeneity of wood-pasture landscapes (Bergmeier et al. 2010; Oldén et al. 2017). The common adverse effect of these land-use changes is the loss of semi-open, mosaic habitat structure, which is indeed the key driver of the biodiversity found in wood-pastures, often higher than that of closed forests or agricultural fields (Hartel et al. 2014). Thus, Chapter 4 and 5 present further evidence that the loss of habitat heterogeneity has adverse consequences for biodiversity, ecosystem functioning and the provision of services in wood-pastures (Bereczki et al. 2014).

A positive influence of reducing management on biodiversity has been shown for particular taxa including birds, mostly resulting from the higher availability of feeding and nesting resources provided by woody vegetation (Barbaro et al. 2014). However, the negative consequences for some other functional guilds from low management or abandonment suggest that the impacts of management intensity should be considered from broader perspectives as it is discussed in detail in Chapters 4 and 5. Moreover, the niche requirements of forest bird guilds may be still maintained by preserving the adequate shrub and tree layers in pasture by adjusting non-intensive management strategies, as demonstrated in Chapters 4 and 5. This is in line with the principle that in general conservation efforts should aim at increasing diversity of multiple taxa, rather than favouring a single taxon or functional

group, to ensure biodiversity-rich habitats and healthy ecosystem functioning and services in human-shaped habitats (Queiroz et al. 2014; Mauerhofer et al. 2018).

Finally, as referred before (Gagic et al. 2015) there may be mismatches between taxonomic and functional responses of birds to the changes in habitat variables. The results of this thesis support the advantages of assessing the functional diversity of various response and effect traits, to provide more complete insights on the dynamics of the relations between species and on ecosystem processes (Vandewalle et al. 2010; de Bello et al. 2010). Chapter 5, in particular, emphasizes how the study of the response of effect traits to land-use changes may provide insights on ecosystem service provision and inform managers and decision-makers about the future of wood-pasture ecosystem services under different changes in management strategies.

Limitation of the thesis and future research directions

Despite the important results described above, it should be noted that further research is needed to confirm its results and overcome some of the limitations associated with this work. To begin with, the analyses presented in Chapters 2 and 3 should be replicated with a larger sampling effort to validate some of the results observed for which the low sample size may have prevented the observation of statistically significant differences. Also, the inclusion of year-around sampling for multi-species, particularly using different sampling methods such as sweep nets and light traps for arthropods, can improve the robustness of the findings. Moreover, it would be desirable to study to what extent the positive influences of shrubby patches on biodiversity, here observed for the most common type of western Mediterranean wood-pastures, is applicable in distinct types of woody-pastures.

Our findings of Chapters 2 and 3 also suggest that the presence of shrubs changes microhabitat conditions as suggested by the observed differences in the functional identities of beetles and lichens

found in these patches. However, future research should assess these environmental variations in greater detail by using direct measurements of micro-climate parameters such as temperature, moisture and shade rate. In addition, most of the traits explored in Chapter 3 are both response and effect traits such as plant woodiness, beetle body size or lichen growth forms. Therefore, considering the differences observed in both the functional diversity and composition of these taxa, future studies may explore in detail the potential existence of variations in the ecosystem services provided by woody plants (Lavorel 2013b), beetles (Noriega et al. 2017) and lichens (Zedda and Rambold 2015) that are closely associated with those traits.

Lastly, concerning Chapters 4 and 5, further efforts should focus on year-around bird sampling to provide additional insights on how wintering bird communities respond taxonomically and functionally to changes in management intensity. This may also provide information on how different ecosystem services and dis-services provided by birds may be influenced by different land-uses. Finally, changes to natural pest control by birds in response to land-use changes should be evaluated directly through a comprehensive study design aimed at testing specific relations in bird-pest trophic networks.

Concluding remarks and implications for management and conservation

Overall this thesis underlines two major findings. Allowing shrub development within small patches stimulates habitat heterogeneity and substantially increases the taxonomic and functional diversity of multiple taxa. However, generalized shrub growth resulting from lower management intensity homogenizes the habitat structure and leads to the loss of particular bird and trait assemblages, potentially resulting in a reduced provision of specific ecosystem functions and services in wood-pastures.

The higher presence of shrubs in ungrazed patches provides a distinct micro-habitat which facilitates the presence of different species and trait assemblages of plants, beetles and lichens when compared to the pasture matrix as revealed in detail in Chapters 2 and 3. The shrubby patches cover less than 0.5% of the study areas, implying that preserving and even expanding these patches requires minimal losses from areas devoted to agriculture or grazing. Moreover, establishing the patches should be practical considering the high regenerative abilities of native shrubs which together makes this strategy a low-cost and efficient conservation action for wood-pastures. However, it should be noted that there are several issues such as inbreeding risk and vulnerability of local extinction requiring further consideration in the case of establishment of the shrubby patches (Rey Benayas et al. 2008).

This thesis also indicates that non-intensive regular management may preserve habitat heterogeneity facilitating the presence of diverse bird trait assemblages that result in higher functional diversity when compared to less managed areas (Chapters 4 and 5). Elimination or near elimination of grazing transforms the characteristic semi-open, heterogeneous habitat structure of wood-pastures into somewhat homogenous, dense shrublands, which favour only a subset of bird guilds and results in lower functional diversity due to the loss of guilds, such as ground-foragers, with important roles in natural pest control. Actively grazed areas, however, as long as they are able to maintain a heterogeneous habitat structure, can preserve a greater diversity of guilds, as observed in Chapters 4 and 5. Ensuring the availability of adequate niches for bird species adapted to more closed-canopy habitats in actively managed areas, can mitigate the observed declines in relative abundances of these groups while still supporting the presence of grassland birds. At this point, our results may emphasize the importance of multiplying or expanding the shrubby patches, considering that they resemble the vegetation structure of closed-canopy forests, and may thus enhance the presence of forest bird guilds without substantially requiring the abandonment of grazing.

In summary, this work suggests that maintaining shrubby patches and non-intensive regular management in wood-pastures can be two important management strategies that enhance habitat heterogeneity, multi-species biodiversity and ecosystem processes. We should also note that maintaining habitat heterogeneity is itself an important ecosystem service which contributes to the regulation and maintenance of healthy environmental conditions and to boost habitat resilience (Fischer et al. 2006; Moreno et al. 2018). Therefore, efforts in preserving habitat heterogeneity may contribute more to wood-pastures than short-term increases in biodiversity and ecosystem functioning. The main management implications supported by this thesis, which presents evidence from ecological data to support various potential improvements in the management in wood-pastures, can be suggested for inclusion in valuation and certification schemes, such as the High Nature Value (HNV) farmland framework, the Forest Stewardship Council (FSC) certification scheme and Payment for Ecosystem Services (PES). However, we underline that preserving the sustainable balance of biodiversity and economic values of wood-pastures is a very complex management issue, that involves not only various ecological components but also social and economic issues that were not addressed in this thesis.

The substantial contribution of multi-taxa and functional diversity approaches to this study should be highlighted, as it allowed a better understanding of how species from multiple taxonomic groups respond to and affect the habitat in various ways, and how these interactions vary across land-use driven changes in wood-pastures. Exploring the multiple approaches for the sustainable human-use of nature in social-ecological systems is a long-term research area and the communication between the scientific community and the land managers as well as policy-makers is a vital component of these efforts (Mauerhofer et al. 2018). In conclusion, this thesis provides specific recommendations on how to promote biodiversity-friendly management in wood-pastures preserving the semi-open and heterogeneous habitat structure that harbour diverse species and trait assemblages of multi-taxa enhancing ecosystem processes.

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